1-1-2006

Fine-root biomass and dynamics of six tropical tree species

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Fine-root biomass and dynamics of six tropical tree species

by

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A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Ecology and Evolutionary Biology

Program of Study Committee:
James Raich, Major Professor
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Ames, Iowa

2006

Graduate College

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ABSTRACT

Estimations of fine-root storage and dynamics have been lacking in most ecological studies in tropical forests, deterring proper quantification of productivity in this biome. My thesis addresses this issue by exploring fine-root biomass and growth rates for six tropical tree species. The study was conducted in the Caribbean lowlands of Costa Rica and included five native species (*Hyeronima alchorneoides*, *Pentaclethra macroloba, Virola koschnyi, Vochysia ferruginea* and *Vochysia guatemalensis*) and one exotic (*Pinus tecunumanii*), grown as single-dominated, 16-year-old plantations. The main objectives in my study were (1) to describe fine-root systems, in terms of size and vertical distribution, fine-root growth rates and fine-root carbon and nitrogen content for the six species and (2) to compare fine-root carbon dynamics, with other carbon fluxes in the plantations such as aboveground litterfall and soil-CO_2 emissions.

Chapter two addresses the first objective. Fine-root systems were shallow, with > 75% of the total fine-root biomass situated in the uppermost 30 cm of the soil in all the species. Moreover, species showed differences in biomass only in the upper 15 cm layer, ranging from 182 g m^{-2} in *Pinus tecunumanii* to 433 g m^{-2} in *Hyeronima alchorneoides* plots, on average. Fine-root growth, assessed with ingrowth cores, ranged from 304 g m^{-2} yr^{-1} in *Virola koschnyi* to 1308 g m^{-2} yr^{-1}in *Hyeronima*, which are moderate to high rates in comparison with root ingrowth rates reported in the tropics. I tested the hypothesis that fine-root lifespan would follow trends already described for leaf tissues. In contrast to the negative relationship between tissue longevity and nitrogen concentration found in leaves, fine-root lifespan among species was not correlated with root nitrogen concentration. Additionally, ingrowth rates were positively correlated with root C:N ratio, which contradicts

the described trend in leaves. Results did not support the hypothesis that fine root longevity is related to root nitrogen concentration among species.

Chapter three explores the relationships among fine-root growth, aboveground litterfall and soil respiration. Species differed in allocation patterns; *Hyeronima alchorneoides* and *Vochysia guatemalensis* had similar aboveground litter and fine root production, whereas *Pinus tecunumanii* produced substantially more aboveground litter than fine roots. Mean total detritus production was higher in *Hyeronima* and *V. guatemalensis* plots with 1210 and 1030 g C m^{-2} yr^{-1} respectively, than in *Virola* and *Pinus* plots with 690 and 720 g C m^{-2} yr^{-1} respectively. Soil-CO_2 emissions ranged from 1610 g C m^{-2} yr^{-1} in *Pinus* to 2365 g C m^{-2} yr^{-1} in *V. guatemalensis*. Soil-CO_2 emissions were marginally correlate with fine-root ingrowth ($P = 0.06$) but not with fine litterfall ($P = 0.26$), suggesting that fine-root detritus production is an important factor explaining soil-CO_2 emissions at least at local scales. Rhizosphere respiration, estimated as the difference between annual detritus production and soil respiration, was similar among species and contributed 52% of the total soil-CO_2 flux estimated on average. Similarities in belowground carbon allocation and rhizosphere respiration among species indicated that these tropical tree species have similar metabolic activity belowground despite the substantial variation in root production.

CHAPTER 1. GENERAL INTRODUCTION

INTRODUCTION

Despite the fundamental role of fine root dynamics in terrestrial ecosystems, fine roots have been ignored in many efforts to quantify net primary productivity (NPP). Fine root growth comprised more than half of NPP in temperate broadleaf (Hendrick and Pregitzer, 1993; Fahey and Hughes, 1994), coniferous (Vogt *et al.*, 1983), and boreal forest (Ruess *et al.*, 2003) and as much as 70% in some savannas (House and Hall, 2001). Mean residence time for organic matter on those ecosystems might be reduced by 50% if fine root turnover is considered (Vogt *et al.*, 1983). Fine roots also provide an important amount of detritus organic inputs to mineral soils in most biomes, playing a prominent role in the ecosystem nutrient cycling and carbon storage (Aerts *et al.*, 1992; Jackson *et al.*, 1997; Gill and Jackson 2000).

There is increasing evidence that changes in diversity and especially the dominance of a single species in otherwise more diverse ecosystems could have striking effects on ecosystem functioning and stability (Tilman *et al.*, 1996; Hooper and Vitousek, 1997; Naeem and Li, 1997). Even so, our knowledge about the effect of species dominance in belowground ecosystem functioning is poor, albeit some studies do suggest that species identity might be important. For instance, Aerts *et al.* (1992) reported that nutrient availability in infertile ecosystems depended strongly on fine root turnover. Nutrient release rates from fine roots differed substantially among species with some species accounting for 20% and other for up to 70% of the total N and P available in the soil. Coleman *et al.* (2000), comparing

belowground processes between pine and poplar stands, reported higher soil CO_2 efflux and root longevity in the pine plantation whereas fine root production was substantially higher in the poplar stand. They concluded that differences between the species generated variations in nutrient availability between stands.

Tropical rain forests are critical ecosystems in terms of the global carbon cycle, they account for 52% of the world's forest coverage (FAO, 2003), contain approximately 55% of the world's biomass carbon and provide 35-45% of the global NPP (Schlesinger, 1997; Grace *et al.*, 2001; Saugier *et al.*, 2001). In addition, approximately 14% of the world's soil carbon is located in tropical areas (Jobággy and Jackson, 2000). Therefore, a slight change of these pools could have significant impact on the global carbon cycle. In fact, tropical deforestation currently adds 1.6-2.4 Gt C to the atmosphere each year and is the second largest anthropogenic source of atmospheric C, surpassed only by fossil fuel emissions (Houghton, 2004; Grace *et al.*, 2001).

Human intervention in tropical areas has produced a highly altered landscape where introduced species (Vitousek *et al.*, 1987), secondary succession (Chazdon *et al.*, 2003) and plantations (Lugo, 1997) have taken a prominent role. Plantations, for instance, currently cover more than 76 million hectares and they are expanding by around 5.4 million ha each year (FAO, 2003). Reforestation through plantations on abandoned and degraded agricultural lands in the tropics has been proposed as an effective approach to sequester atmospheric carbon (Montagnini and Porras, 1998; Binkley and Resh, 1999; Houghton *et al.*, 2000). Several studies have shown that different species in tree monocultures vary in aboveground production (Cuevas and Lugo, 1998; Haggar and Ewel, 1997; Piotto *et al.*, 2003), nutrient use efficiency (Smith *et al.*, 1998; Hiremath *et al.*, 2002), nutrient cycling and conservation

(Stanley and Montagnini, 1999; Bigelow *et al.*, 2004), subsequent regeneration (Powers *et al.*, 1997) and allocation patterns (Binkley and Ryan, 1998). Therefore, species identity may play a major role in the stand efficiency sequestering atmospheric carbon.

Soil organic carbon is substantially affected by differences in fine-root production and tissue quality among tree species (Russell *et al.*, 2004). Even so, fine-root growth, turnover rates and chemical tissue composition remain unknown for most planted species. The objective of this thesis was to determine the influence of species identity on fine-root dynamics. To address our objective we studied six Neotropical tree species in 16-year-old plantations where climate, soil and land use history were uniform.

THESIS ORGANIZATION

This dissertation is arranged into four chapters: Chapter 1, General introduction; Chapter 2, Fine-root mass, growth and nutrient content for six tropical tree species; Chapter 3, Relationships among litterfall, fine-root growth and soil respiration for five tropical tree species; and Chapter 4, General conclusions. Chapter 1 sets the conceptual basis for my research and provides a general layout of the remaining thesis by explaining when and where the studies were conducted, and includes a brief review about the studied species. Chapters two and three comprise the main body of the work, with each chapter representing an individual investigation prepared for journal submission. Chapter four summarizes the main findings from chapters two and three and proposes future research on fine-root dynamics.

Site description

I conducted this research from May 2004 through July 2005 in the La Selva Biological Station (10° 26'N, 83° 59'W) in the Atlantic lowlands of Costa Rica. The site is a moist tropical forest with annual precipitation ranging from 2900 to 6000 mm (3960 mm as average), and an average of > 150 mm of precipitation every month (Sanford *et al.*, 1994). The mean temperature is 25.8 °C with minimal variation across the year. The plantations were established in 1988 on a recently abandoned pasture that had been grazed intensively for approximately 25 years. The plots occupy a hilly upland area with elevations of 44-89 m and soils derived from highly weathered basaltic lava mudflows (Schwendenmann, 2002). The soil was classified as Typic Tropohumult, characterized by high organic matter accumulation, low degree of base saturation, high interchangeable acidity and an argillic horizon (Sollins *et al.*, 1994).

Since plot establishment, several studies have focused on ameliorative effects of the planted species on soil fertility (Fisher, 1995); aboveground growth and timber potential (González and Fisher, 1994); and understory diversity among species (Powers *et al.*, 1997, Haggar *et al.*, 1997). Plantations were established in a randomized complete block design with four replicates. Each block contained twelve 0.25 ha plots with 3 × 3 m tree spacing. In this study the two external rows of trees were considered as buffer areas. Measurements were made inside the internal 30 × 30 m square, which was subdivided in four 15 × 15 m quadrants.

Species description

Hyeronima alchoneoides Allemao (Euphorbiaceae) is an emergent tree, reaching 50 m in height and 1.2 m in diameter, in tropical rain forests between 0-1500 m of elevation and 3500-5000 mm of precipitation from Belize to the Amazon basin (Webster, 2001; Jiménez-Madrigal *et al.*, 2002). This species thrives in well-drained alluvial or residual soils (Flores, 1993). Saplings are associated with medium-sized gaps in natural forests whereas adult trees are canopy or emergent components (Clark and Clark, 1992). Its wood is hard, heavy (specific gravity 0.59 - 0.86 g/cm^3), dark, and resistant to fungi and insect attacks (Flores, 1993). Because of good growth and wood quality, the species is widely planted in Costa Rican lowlands and in a minor scale in Honduras (Redondo-Brenes, in press; Flores 1993).

Pentaclethra macroloba (Willd.) Kuntze (Fabaceae/Mimosoidae) is a dominant component in Caribbean lowland forests in Costa Rica and Nicaragua in areas with more than 3500 mm in precipitation and from 0 to 600 m in elevation (Zarucchi, 2001). Individuals have irregularly branched trunks that can reach 30 m in height and 1.3 m in diameter. This species forms dense stands in the study area. In swampy areas it furnishes up to 50% of the total individuals, but dominance decreases in hilly topography (Hartshorn and Hammel, 1994). Regeneration under the canopy is abundant and seedlings endure under shady conditions and grow aggressively in gaps (Finegan *et al.*, 1999). The wood is heavy (specific gravity 0.61 – 0.70 g/cm^3), resistant to pathogens, and widely used in construction (Jiménez-Madrigal *et al.*, 2002). The species does not have strong apical dominance and trees tend to branch profusely in plantations (González and Fisher, 1994).

Pinus tecunumanii Egiluz and Perry (Pinaceae) is the only exotic species in this study. The species is distributed naturally from southern Mexico to highlands in Guatemala

and Honduras and lowlands in Nicaragua (Styles, 2001). The taxonomy of the species is unresolved; the species is closely related to *Pinus oocarpa*, *P. caribaea* and *P. elliottii* with hybridizing among taxa (Richardson, 1998; Dvorak, 2002). Naturally the species forms almost pure pine communities in association with *P. oocarpa* and *P. caribaea,* interspersed with *Liquidambar*. Regeneration is poor and seedlings are shade intolerant (Styles, 2001). Plantations are spread all over Central and South America, Africa and Australia (Richardson, 1998). The wood is yellowish, soft and moderately heavy (specific gravity 0.51-0.56 g/cm^3). It is employed as sawn timber, paper pulp and firewood (Dvorak, 2002).

Virola koschnyi Warb. (Myristicaceae) reaches 30-45 m and 1 m in diameter (Gentry, 2001), in areas between 0 to 500 m in elevation where precipitation ranges from 3500 to 5000 mm from Belize to Panama (Flores, 1992). The species is an important component in unaltered and logged forests and an important food source for mammals and birds (Flores, 1992; Webb, 1997). It reaches the best growth in alluvial soils where it can form pure stands, but is also frequent in clayey and acidic soils (Flores, 1992). The species is planted locally in Costa Rica for timber production (Petit and Montagnini, 2004). Its wood is moderately light (specific gravity 0.44 g/cm^3), infected easily by fungi and used mostly for veneer and plywood products (Flores, 1992).

Vochysia ferruginea Mart (Vochysiaceae) ranges from Nicaragua to Brazil in rain forests (3000 to 5000 mm of precipitation) from the sea level to 1500 m (Miller, 2001). This species can reach 35 m and 80 cm in diameter. It regenerates in open areas and primary successions and occasionally in large gaps into the forest (Finegan *et al.*, 1999). It seems associated to well-drained soils and especially to mountain slopes where it shows the best growth rates (Finegan and Delgado, 2000). Plantations establish successfully even in highly

degraded areas (Petit and Montagnini, 2004). The wood is light with specific gravity of 0.37-0.42 g/cm^3, light brown and used in veneer and furniture construction (Finegan, 1992)

Vochysia guatemalensis Donn. Sm. (Vochysiaceae) ranges from Mexico to Panama in lowlands with more than 3000 mm of annual rainfall (Miller, 2001). Adapted to secondary succession environments, the species flourishes in open areas and establishes successfully in monocultures even in clayey, acid soils with high aluminum content. Therefore, it has been selected as species for use in restoration of degraded pastures (Carpenter *et al.*, 2004). The wood is white, light (specific gravity ~0.35 g/cm^3) and decays easily when expose to moisture (Flores, 1993). It is employed in veneer and low-cost structures (Jiménez-Madrigal, 2002).

In summary, the study species share some similarities as common emergent or canopy timber trees in mature or succesional forest in Central America. Also, excepting *Pentaclethra macroloba*, the species are used for reforestation projects on abandoned pastures throughout the Costa Rican lowlands (Carpenter *et al.*, 2004; Petit and Montagnini 2004). However, when established in plantations, the species vary in aboveground growth rates (Standley and Montagnini, 1999; González and Fisher, 1994), understory conditions (Haggar *et al.*, 1997) and effects on soil fertility (Fisher, 1995), suggesting that they might influence ecosystem processes such as biomass storage, carbon allocation and nutrient cycling. The aim of this thesis is to explore how, and by which mechanisms, these species affect belowground biomass allocation and carbon fluxes, focusing on fine-root accumulation and dynamics.

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CHAPTER 2. FINE-ROOT MASS, GROWTH AND NUTRIENT CONTENT FOR SIX TROPICAL TREE SPECIES

A paper to be submitted to the journal Plant and Soil

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ABSTRACT

Although fine roots might account for 50 % of the annual net primary productivity in moist tropical forests, there are relatively few studies of fine-root dynamics in this biome. We examined fine-root distributions, mass, growth and tissue N and C concentrations for six tree species established in 16-year old plantations in the Caribbean lowlands of Costa Rica. The study included five native species (*Hyeronima alchorneoides*, *Pentaclethra macroloba, Virola koschnyi, Vochysia ferruginea* and *Vochysia guatemalensis*) and one exotic (*Pinus tecunumanii*) arranged in a complete randomized block design (n = 4). Under all species, > 75% of the total fine-root mass was situated in the uppermost 30 cm of the soil. Fine-root biomass and necromass varied significantly among species but only within the uppermost 15 cm, with biomass values ranging from 182 g m^{-2} in *Pinus* to 433 g m^{-2} in *Hyeronima* plots, and necromass ranging from 48 g m^{-2} in *Pinus* to 183 g m^{-2} in *Virola* plots. Root growth, measured using ingrowth cores, differed significantly among species, ranging from 304 g m^{-2} yr^{-1} in *Pinus* to 1308 g m^{-2} yr^{-1} in *Hyeronima*. These growth rates were 1 to 5 times those reported for moist temperate areas. Turnover rates ranged from 1.6 to 3.0 yr^{-1} in *Virola* and *Hyeronima* plots respectively. Fine-root biomass was significantly and positively correlated with fine-root growth (0.79; n= 24) but did not correlate with fine-root turnover (r = 0.10; n = 24), suggesting that fine-root accumulation is a function of growth rates rather than mortality. Fine root longevity was not correlated with root N concentration and fine-root

growth was negatively correlated with root N concentration. Therefore, the trade-off between root dynamics and root nitrogen concentration differ from the negative trend reported globally for foliar N concentration and leaves lifespan. Thus, the assumption that fine-root demography is related to N concentration, as is the way with leaf demography, must be reviewed in tropical ecosystems.

INTRODUCTION

Fine roots account for a significant proportion of energy and nutrient fluxes in most terrestrial ecosystems (Jackson *et al.*, 1997). More than 50% of the annual net primary productivity is allocated belowground in many forests (Vogt *et al.*, 1983; Hendrick and Pregitzer, 1993; Burke and Raynald, 1994; Fahey and Hughes, 1994; Ruess *et al.*, 2003). Nutrient inputs to soils from root litter can be as much as or higher than the return from the aboveground counterpart (Aerts *et al.,* 1992; Sanford and Cuevas, 1996), becoming the main pathway of organic carbon to soil, which is the largest pool of terrestrial carbon (Jobbágy and Jackson, 2000). In moist tropical forests fine-root systems have been described as shallow (Jordan and Escalante, 1980; Gower, 1987; Jackson *et al.*, 1996; but see Nepstad *et al.*, 1994; Canadell *et al.*, 1996), highly variable spatially (Carvalheiro and Nepstad, 1996; Ostertag, 1998) and small in comparison with aboveground biomass (Cairns *et al.*, 1997). Nevertheless, this ecosystem shows the largest root biomass and one of the highest rates of fine-root production globally (Jackson *et al.*, 1996; Vogt *et al.*, 1996; Gill and Jackson, 2000). Even so, measures of fine-root mass and growth have been lacking in most tropical

studies, preventing proper quantification of primary productivity and nutrient cycling in those forests (Clark *et al.*, 2001; Lauenroth and Gill, 2003; Raich *et al.*, 2006).

Plantations in the tropics have been established to meet an increasing demand for soil protection, improvement of soil fertility and ecosystem recovery in parallel with timber demand (Parrota *et al.*, 1997; Kobayashi, 2004). Although several studies in tropical plantations have demonstrated that species differ in important aspects such as tissue quality (Lugo, 1992; Stanley and Montagnini, 1999), nutrient use efficiency (Smith *et al.*, 1998; Hiremath *et al.*, 2002; Bigelow *et al.*, 2004) and growth (González and Fisher, 1994) as well as in their influence on ecosystem traits such as soil fertility (Fisher, 1995) or understory biodiversity (Parrota *et al.*, 1997; Powers *et al.*, 1997), little attention has been paid to fine-root dynamics. Studies that included this component, however, indicate that species vary strongly in growth rates and that these differences significantly affect nutrient availability or soil carbon accrual in ecosystems (Binkley and Ryan, 1998; Russell *et al.,* 2004).

Annual production of fine roots often exceeds their mean standing crop (Gill and Jackson, 2000). Fine root production and mortality appear to occur simultaneously during the year and the standing crops of live and dead roots are only the end products of these processes. In other words, fine-root accumulation in any ecosystem is ultimately controlled by the magnitude of root growth and turnover rates in the system (Santantonio and Grace, 1987). Understanding these processes, production and mortality, thus provides a basis for comparing fine-root dynamics and compare species (Burke and Raynald, 1994; Ruess *et al.*, 2003).

Fine-root dynamics can also be evaluated by assuming similarities with other plant structures (Ryser and Lambers, 1995; Espeleta and Donovan, 2002). Leaves, for example, are

hypothesized to balance growth rates, nitrogen concentration and longevity in order to maximize resource acquisition (Bloom *et al.,* 1985). Fast-growing leaves tend to have relatively high nitrogen concentration and short lifespan, whereas slow-growing leaves have relatively low nitrogen concentrations and slower turnover rates (Poorter *et al.*, 1990; Reich *et al.,* 1992; Reich *et al.*, 1997). Although it has been proposed that leaves and fine roots follow the same trade-off (Eissenstat, 1992; Eissenstat and Yanai, 1997; Eissenstat *et al.*, 2000) little is known about the relationship between growth rates, nitrogen concentration and lifespan in fine roots, especially in tropical woody species (Pregitzer *et al.*, 2002).

In this study we examined fine roots in single-species plantations of six tropical tree species (Table 1). Our objectives were to compare these species in terms of fine root vertical distribution, biomass, C and N concentrations, growth, and turnover rates. We hypothesized that fine-root biomass would be positively related to root production across species. Further, we would expect that live fine root N concentration would correlate negatively with mean fine-root lifespan, and positively with root growth across species, following trends previously described for foliar tissues (Poorter *et al.*, 1990; Reich *et al.*, 1997).

METHODS

Study site

Field studies were conducted at La Selva Biological Station, in the Atlantic lowlands of Costa Rica (10° 26'N, 83° 59'W). Mean annual rainfall is 3960 mm with an average of >150 mm of precipitation every month (Sanford *et al.*, 1994). The mean temperature is 25.8 °C with minimal variation across the year. The experimental plantations were established in

1988 on a recently abandoned pasture that had been grazed intensively for approximately 30 years. The plots occupy a hilly upland area with elevations of 44-89 m. The soil is classified as a Typic Tropohumult (Ultisol) and is characterized by high organic content, low degree of base saturation and high exchangeable acidity (Sollins *et al.*, 1994).

Originally the experiment included 11 tree species planted in monoculture and one unplanted control area established in a complete randomized block design with four replicates (González and Fisher, 1994; Fisher, 1995). Each block contained twelve 0.25-ha plots with 3 × 3 m tree spacing. Soil base line data were collected in 1987, before tree planting, and tree diameters and height were measured from 1988 to 1994 (González and Fisher, 1994). There were no maintenance activities between 1995 and 2002.

The six species considered in this study were *Hyeronima alchorneoides* Allemao, *Pentaclethra macroloba* (Willd) Kunth., *Virola koschnyi* Warb, *Vochysia ferruginea* Mart., *Vochysia guatemalensis* Donn. Sm., and the exotic species *Pinus tecunumanii* Egiluz and J. P. Perry. They vary in traits such as aboveground growth rates (González and Fisher, 1994), canopy height (Haggar *et al.*, 1997), understory regeneration (Powers *et al.*, 1997) and rooting depth (Fisher, 1995) (Table 1). The native species are harvested from natural forests for timber purposes and, except for *P. macroloba*, which is the dominant species in local forests (Hartshorn and Hammel, 1994), all of them are grown in plantations for timber production. *Vochysia guatemalensis*, *V. ferruginea* and *Hyeronima alchorneoides* are the main species in Costa Rican reforestation projects whereas *Virola koschnyi* is planted just locally (Piotto *et al.*, 2003; Petit and Montagnini, 2004). *Pinus tecunumanii* is not planted in the region but it is extensively cultivated at higher elevations (Dvorak, 2002).

Analysis of fine-root biomass and depth distribution

In each of the plots the two external rows of trees were buffer areas in which no sampling was done. Measurements were made inside the internal 30 × 30 m square, which was subdivided into four 15 × 15 m quadrants. Samples were distributed evenly among quadrants to maintain representative plot sampling. Sample location inside each quadrant was randomly selected. Standing stock of fine roots was determined by collecting with a metal corer six soil cores, 15 cm deep by 5.35 cm in diameter, in each plot (24 samples per treatment). Samples were collected twice (May to July in 2004 and again May to July in 2005). In addition, we sampled to 30 cm for one sample per plot in 2004 and three samples per plot in 2005, to determine fine-root mass differences between 0-15 and 15-30 depths. Fine-root mass located below 30 cm depth was determined by sampling from the walls of soil pits dug for another study. A single 1.00 × 0.75 m soil pit was excavated in each plot between February and April 2005. From each pit, four aluminum cylinders (150-ml volume each) were inserted into the wall of the pit, spaced evenly along the depth interval, to sample a total of 600 cm^3 per depth interval. Leaf-cutter ants (*Atta cephalotes*) have active nests on the plots; obvious nests were excluded in all pit sampling.

All samples were placed in plastic bags, refrigerated immediately upon return to the lab and processed within two days following harvest. Each core was soaked at least two hours, most of them for 12 hours, before being processed in a hydropneumatic elutriation system with 530-μm mesh filters. We defined fine roots as all non-woody roots, most of which were < 2 mm in diameter. *Hyeronima* and *Virola* produced non-woody, succulent roots >2 mm in diameter. Fine roots were sorted as live or dead based on visible appearance, texture, color and friability, oven-dried to 65 °C and weighed to an accuracy of ±0.0001 g. Although the

planted species were still dominant, they were not strictly monocultures, in that the plots contained other species regenerating beneath the canopy. We did not sort roots by individual species, so it must be noted that for all variables measured, the effect of 'species' refers to the entire treatment effect of the planted species, including the contribution from understory regeneration.

Analysis of fine-root ingrowth

We measured fine-root ingrowth by installing five 15-cm deep, 5.35-cm diameter ingrowth cores per plot (20 cores per treatment). Ingrowth cores were constructed of polyethylene tubing (8-mm mesh size) with 2-mm nylon mesh screens for tops and bottoms. Cylinders were filled with sieved root-free soil extracted from the same plot; cylinders were packed at the same density as the soil. An earlier study in La Selva demonstrated that four-month intervals were optimal for assessing ingrowth (Russell *et al.*, 2004). Thus, root-free cores were installed three times in this study: June 2004, November 2004 and, March-April 2005 and removed systematically the following November 2004, March 2005, and June-July 2005. During extractions, roots outside the cylinders were cut flush and discarded. The samples were then processed in the same manner as biomass samples, except that we did not sort into live and recently senesced roots. We defined annual ingrowth production as the sum of ingrowth mass measured over the three seasons corrected to 365 days. Fine-root turnover was determined as annual fine-root ingrowth divided by the fine-root biomass at 0-15 cm depth (Gill and Jackson, 2000).

Tissue chemistry analysis

Tissue chemistry was characterized for each treatment by analyzing live and dead roots for C and N concentration. For the biomass study, roots sampled from all the quadrants within the same plot each year were combined and ground; live and dead roots were kept as separate fractions. Ingrowth roots (live + senesced) within each plot were similarly combined and ground in each measurement. Carbon and N contents were determined using a CE Elantech Flash EA 1112 C-N elemental analyzer (CE Instruments, Milan, Italy). All data presented as 65°C dry weights.

Statistical analyses

Vertical root distribution was modeled by the equation:

$$Y = 1 - \beta^d \quad (1)$$

(Gale and Grigal, 1987) where d is depth (cm) and Y is the proportion of roots from the surface to depth d, and β is a numerical index of rooting distribution. High values of β indicate greater proportion of roots with depth (Jackson *et al.*, 1997). Differences among species in root distribution were tested with linear regression analysis for the log-transformed β data. Species-specific differences in total fine-root biomass (0-100 cm depth) and dead:live root ratio were evaluated using analysis of variance (ANOVA). For several response variables, a repeated-measures ANOVA was applied, with species and block as the main factors, their interaction as a random factor, and time as the repeated measure factor. The fine-root response variables (all 0-15 cm) included: live and dead mass; root nitrogen and carbon concentration and C:N ratios; and ingrowth rates. Only the dead mass variable was square root transformed to meet the ANOVA assumptions of normal distribution of residuals

and equality of variance. When effects were significant, multiple comparisons were made using the Tukey-Kramer HSD test ($\alpha = 0.05$).

If fine-root biomass is a function of root production, then differences in fine-root accumulation among species would be correlated significantly with differences in ingrowth rates. Alternatively, if mortality is the main factor explaining variation in fine-root accumulation we would expect a significant correlation between root biomass and turnover rates. We tested these alternatives using a pair-wise correlation analyses between ingrowth rate and turnover with fine-root biomass using mean values from each plot ($n = 24$). Also, we performed a similar analysis between fine-root necromass and fine-root ingrowth rates, assuming that mortality would equal root growth inputs among species. There were no differences observed in total fine-root mass between years (see below). To test our second hypothesis, pair-wise correlation analyses were performed to evaluate the relationship between fine-root nitrogen concentration with fine-root ingrowth and mean fine-root lifespan as well as the relationship between C:N ratio with fine-root ingrowth rates. All statistical analyses were performed using JMP Data Analysis software (version 5.1.2, SAS Institute, NC, USA).

RESULTS

Fine-root vertical distribution, biomass and necromass

All the species had relatively shallow fine-root systems with 77 to 89% of the total mass (live plus dead) situated in the upper 30 cm. Fine-root mass declined exponentially with depth for all species with β values averaging 0.943. *Hyeronima* plots had the lowest index of rooting distribution with 0.941 whereas *Pinus* had the highest with 0.946, but values of β did not differ significantly between those two species ($P = 0.36$; Figure 2.1). The index of rooting distribution in our plots ($\beta = 0.943$) was lower than the value estimated for tropical evergreen forest ($\beta = 0.962$; Jackson *et al.*, 1996), suggesting that fine-root systems in our plots are relatively shallower than the average for this biome.

Total fine-root mass as well as live:dead proportion was different among species but only in the uppermost 15 cm ($P < 0.0001$ for total fine-root mass; $P = 0.006$ for live:dead ratio; Table 2.2). The total amount of roots in the uppermost layer did not differ significantly between years ($P = 0.26$) but the ratio between live and dead fine-roots did ($P < 0.0001$). All the species had more necromass in 2005 than in 2004, albeit it was significant only for *Vochysia guatemalensis* and *V. ferruginea* (t-test; $P < 0.01$ for both species; data not shown). Evident tree mortality in *V. ferruginea* plots could increase the amount of dead roots for this species in the second year. Moreover, difficulties determining dead and live roots in those two species could explain partially the necromass increase in the second year.

Hyeronima plots with 602 g m^{-2} had the largest total fine-root biomass although it was not significantly different from *Virola* or *V. guatemalensis* plots, which contained 597 and 580 g m^{-2} respectively. *Pinus* plots with 286 g m^{-2} had significantly lower fine-root biomass

than *Hyeronima*, *Virola* and *V. guatemalensis* plots but similar to *Pentaclethra* and *V. ferruginea* plots, which had 488 and 392 g m^{-2} on average, respectively (Tukey-Krammer HSD test; $P < 0.05$; Table 2.2). *Virola* plots had the highest fine-root necromass, which accounted for 29% of the total fine-root mass. Dead fine roots in *V. guatemalensis* plots comprised only 13% of the total fine-root mass, the lowest proportion among species ($P<0.005$; Table 2.2). The dead:live root ratio was on average higher in *Virola* (0.40) than in *V. guatemalensis* plots (0.15) whereas the remaining species had intermediate values (Tukey-Krammer HSD test; $P < 0.05$; Table 2.2).

Fine-root ingrowth and turnover rates

Ingrowth rates in the uppermost 15 cm did not differ through time under any of the species ($P = 0.30$), indicating no seasonality in root growth. Species differed significantly in fine-root growth rates, however ($P = 0.0001$; Table 2.4). *Hyeronima* and *V. guatemalesis* plots had the highest ingrowth rates, up to 1300 g m^{-2} yr^{-1}, 3.4 times higher on average than that of *Pinus* plots. Across species, fine-root ingrowth rate was correlated with fine-root biomass ($P < 0.0001$, $r = 0.79$, n = 24; Figure 2.2) but uncorrelated with necromass ($P = 0.20$, $r = 0.26$, n = 24), suggesting that fine-root biomass was closely related to growth rates but dead fine-root mass was not related to the detritus inputs. Turnover rates also differed among species ($P = 0.03$) with rates in *Hyeronima* plots nearly twice as fast as those of *Virola* (Tukey-Krammer HSD test; $P < 0.05$; Table 2.4). The remaining species had intermediate values. Turnover rates were uncorrelated with fine-root biomass across plots ($P = 0.63$, $r = 0.10$).

Root C and N concentration

Live root N concentration decreased with depth ($P > 0.0001$), which is consistent with observed trends in temperate broadleaf fine-root systems (Pregitzer *et al.*, 1998). Among species, live root C and N concentrations were significantly different in the uppermost 15 cm ($P < 0.0001$ for both elements; Table 5). Average live root N concentration was 1.67% among species. *Pentaclethra,* a N-fixing tree, had the highest root N concentration while those in *Hyeronima* had the lowest (Tukey-Krammer HSD test; $P < 0.05$; Table 5). Carbon concentration averaged 44.8% among species with the highest values in *Virola* and *Pentaclethra* plots (Tukey-Krammer HSD test; $P < 0.05$; Table 5). The C:N values were relatively narrow for fine roots. Indeed, the C:N ratio range in this study (22-32) was narrower than the global average reported for ≤2 mm in diameter fine roots (Jackson *et al.*, 1997; Gordon and Jackson, 2000) but similar to ratios reported for first- and second-order roots of temperate broadleaf species (Pregitzer *et al.*, 2002). Total N in root systems averaged 5.34 g N m^{-2} in the uppermost 15 cm, differing significantly among species. *Vochysia ferruginea* and *Pinus* plots had the lowest fine-root N stocks (4.33 and 2.91 g N m^{-2} respectively;Tukey-Krammer HSD test; $P < 0.05$; Table 2.3).

Fine-root growth was negatively correlated with fine-root N concentration ($P < 0.0001$, $r = -0.78$, n = 24; Figure 2.3) contrary to the hypothesized trend based on patterns described for leaves. Further, ingrowth rates were positively correlated with root C:N ratio ($P < 0.0001$, $r = 0.84$; n = 24; Figure 2.2) but not with C concentration ($P < 0.0001$, $r = -0.78$, n = 24), suggesting that the variation in root N, but not C, explains differences in fine-root growth rates among species. Mean fine-root lifespan was not correlated with live fine-root N

concentration ($P = 0.34$, $r = 0.20$; n = 24; Figure 3) across species, which is inconsistent with our hypothesized negative correlation between root N concentration and root lifespan.

DISCUSSION

Our objectives were to describe fine root systems in terms of vertical distribution, mass and root growth rates in single-species plantations of six tropical trees. Further, we determined fine-root carbon and nitrogen concentrations to test whether fine-root turnover were related with root nutrient status in the same way that it has been described for leaves.

Vertical distribution and mass of fine roots

Consistent with previous studies in moist tropical forests, fine-root biomass decreased exponentially with soil depth (Raich, 1983; Cairns *et al.*,1997; Jóbaggy and Jackson, 2000), nonetheless the profile distribution of roots for all the species in this study was shallower than previously reported in tropical evergreen forests (Jackson *et al.*, 1997). Sollins *et al.* (1994) reported that the clay content in this soil (Matabuey consociation) increased from 41% in the A horizon (0-18 cm) to 62% in the underlying argillic horizon, which parallels the abrupt decrease in root biomass observed for all the species. Further, the soil organic carbon content among plots had a similar trend with the highest values in the first 15 cm and an exponential decline with depth (Russell *et al.*, submitted). These data suggest that increasing clay content with depth might impede fine-root growth deeper in the profile. Thus, we hypothesize that soil texture plays a role in confining fine-root growth to a shallow depth, and that this abiotic factor overrides species-specific differences in rooting patterns.

Fine-root biomass in the upper 15 cm in all study plots averaged 328 g m^{-2} (Table 2.2), which is higher than previous values at similar depth for fine-root biomass in La Selva (Raich, 1980; Gower, 1987) but consistent with the averaged 330 g m^{-2} reported for tropical evergreen forests (Jackson *et al.*, 1997). The low biomass values observed in the *Pinus* plots are consistent with other tropical studies that compared fine root biomass in *Pinus* plantations with broad-leaved species (Cuevas *et al.*,1991; Cavelier and Santos, 1999). Values for fine-root biomass (≤2 mm) among broadleaf species were similar to those reported by Parrota (1999) in 9 year-old *Eucalyptus robusta, Leucaena leucocephala,* and *Casuarina equisetifolia* plantations, Cuevas *et al.*, (1991) in a 11 year-old secondary forests and Klinge and Herrera (1973) and Silver and Vogt (1993) in primary forests respectively; all located in similar soils (Ultisol-Oxisol) and depth.

Similarities in fine root biomass among plantations and secondary forest suggests that tropical tree stands may quickly accumulate a steady amount of fine roots, which could be similar to mature forest (Raich 1980). Nevertheless, several authors had found consistent differences in fine root biomass between adjacent succesional and mature forests, even after several decades of succession (Sanford, 1989; Cavelier *et al.*, 1996; Hertel *et al.*, 2003). The differences are normally attributed to stand age rather than species composition. The significant positive relationship between fine-root growth and biomass that we found indicates that species-specific variations in fine-root growth contribute to stand-level differences in fine-root biomass. In addition, total fine-root mass was constant between years, suggesting that the differences among species in fine-root stocks are steady. Thus, we conclude that species identity is a main factor explaining fine-root biomass differences among stands and could play an important role in tropical forests, especially in secondary

succession where a single species can account for most of the stand biomass (Guariguata and Ostertag, 2002).

Fine roots dynamics

The ingrowth core technique has been recommended for estimating root productivity in fast-growing root systems (Vogt *et al.*, 1998) and has been repeatedly used in tropical soils (Jordan and Escalante, 1980; Cuevas and Medina, 1988; Cuevas *et al.*, 1991; Raich *et al.*, 1994; Russell *et al.*, 2004). Among our studied species, fine-root ingrowth rates averaged 754 g m^{-2} yr^{-1}, which is in the upper range of rates observed in tropical ecosystems (Lauenroth and Gill, 2003). Similar to results from temperate (Aerts *et al.*, 1992; Coleman *et al.*, 2000; Espeleta and Donovan, 2002; Matamala *et al.*, 2003) and tropical areas (Binkley and Ryan, 1998; Russell *et al.*, 2004), tree species differed substantially in root growth. The slow root growth rates observed for *Pinus* in this study were similar to other tropical *Pinus* ingrowth rates in plantations (Cuevas *et al.*, 1991). The high root growth rates we observed for other species, notably *Hyeronima* and *V. guatemalensis* with more than 1000 g m^{-2} yr^{-1}, were similar to those reported in Amazonian forests growing on highly weathered soils (Cuevas and Medina, 1988; Sanford and Cuevas, 1996).

High fine-root growth was coupled with rapid turnover rates. Although rapid fine root turnover is expected in tropical lowlands (Lauenroth and Gill, 2003), the observed rates in this study, which ranged from 1.6 to 3.9 yr^{-1}, were higher than those reported for other tropical forests (average 0.8 yr^{-1}; Gill and Jackson, 2000). In fact, mean turnover coefficient for *Hyeronima* and *V. guatemalensis* plots are among the highest ever reported. Cuevas and Medina (1988) found that fine-root growth rates were considerably higher on weathered soils

because nutrients such as Ca, P and Mg can be easily leached or occluded in these soils. So, roots systems must be highly dynamic and shallow in order to capture nutrient from fresh litter (Jordan and Escalante, 1980; Whitmore, 1998). A consequence of a shallow root system is that it increases the exposure of roots to higher temperatures, drought, physical damage and pathogens; therefore decreasing their lifespan (Eissenstat *et al.*, 2000). These concepts are consistent with our findings.

Although there is evidence that fine-root dynamics vary among tree species (Aerts *et al.*, 1992; Coleman *et al.,* 2000; Matamala *et al.*, 2003), most studies in the tropics have focused on external factors controlling root appearance and disappearance, such as nutrient availability (Giardina *et al.*, 2004), soil moisture (Yavitt and Wright, 2001), rainfall seasonality (Green *et al.*, 2005) or litterfall inputs (Sayer *et al.*, 2006) rather than in inherent differences among species in root production and longevity. This study demonstrated that tropical tree species vary in fine root production. Further, it indicated that live fine-root mass is closely related to inherent growth rates among species whereas turnover is not, suggesting that root accumulation is controlled by root production rather than mortality or that a external factor affects root growth and root accumulation similarly.

A remarkable result in our study was the differences found among species in necromass. Although Jackson *et al.* (1997) reported that necromass comprises on average 40% of the total fine-root mass in moist tropical forests this compartment is infrequently quantified. In our case fine-root necromass ranged from 13 to 29% of total biomass, with significant differences among species. This indicates that dead roots have accumulated at different rates depending upon the dominant species. Since fine-root biomass was similar among years in this study, fine-root growth and detritus production must be similar. Thus, it

is possible to determine whether fine-root necromass is more a function of dead-root inputs or dead-root decay. We found a poor correlation between fine-root necromass and fine-root ingrowth rates, suggesting that dead-root stocks across species are not related to fine-root mortality. Alternatively, we would expect that decomposition rates might explain differences among species in necromass stocks but our data do not allow us to estimate fine-root decay rates. Root decomposition studies from the tropics are scarce (Silver and Miya, 1994). The data that do exists may be inaccurate due to methodological bias (Dornbush *et al.,* 2002), and provide only scarce reference to species composition (Ostertag and Hobbie,1999); hence, this is a promising field for future research.

Differences in fine-root growth and turnover among species might drive important belowground processes. For instance, Matamala *et al.* (2003) described the impact of fine-root turnover on soil carbon pools for temperate tree plantations. They reported that a *Liquidambar styraciflua* plantation produced 45-50% more fine roots that turned over twice as fast as a coniferous (*Pinus taeda)* plantation, leading to a significant increase in soil C concentration. Fine-root ingrowth rates observed in our 16-yr-old *Hyeronima* plots were 3 to 6 times higher than those reported from two 9-yr-old *Hyeronima* plantations at La Selva on alluvial soils, using identical techniques (Russell *et al.,* 2004), suggesting that soil properties and management have a large effect on fine-root growth rates. Soil organic carbon concentrations in those plots were between 33 and 37 g kg^{-1} compared with 49 g kg^{-1} in our plots (Russell *et al.,* submitted), suggesting a proportional relationship between fine root carbon inputs and SOC accrual.

Nutrient availability might also be influenced by fine-root dynamics and tissue traits. For instance, live fine-root N mass was similar between *Hyeronima* and *Virola* plots and

relatively lower than that in *Pentaclethra* plots. When fine root turnover is considered, however, *Hyeronima* plots cycled the largest amount of N via fine root inputs to the ecosystem whereas *Pentaclethra* and *Virola* plots cycled on average 20 and 40% less N respectively. Differences detected in dead root accumulation could also affect nutrient availability. The presence of dead roots may influence not only mineralization rates but also the dominant forms of N in the soil (Ehrenfeld *et al.,* 1997), which would have an important role in nitrogen availability (Roy and Singh, 1995) and soil biological activity (Wardle *et al.*, 2004). Further investigation is necessary to understand the extent to which dominance of single tropical species can modify those processes.

Root dynamics and N content

Although the use of arbitrary root diameter have been broadly discussed for functional comparisons among species (Pregitzer *et al.,* 1997; Majdi *et al.,* 2005) the similarity in fine root turnover and C:N ratio range among species suggest that we are considering similar "modular units" (Pregitzer *et al.,* 2002) and that comparisons are possible.

Because leaves are more readily observed than roots and theories are better developed, trends for leaves have been used as a framework to interpret fine root dynamics (Ryser, 1996; Eissenstat and Yanai, 1997; Reich *et al.,* 1998). Leaf lifespan and growth rates have been repeatedly associated with tissue nitrogen concentration (Reich *et al.,* 1992; Reich *et al.,* 1997). If the same relationship holds for fine roots, then we would expect fine-root lifespan to decline as root N increases among species. The findings in this study, however, did not support this hypothesis. One possible reason for this inconsistency could be the fact

that nitrogen is not a limiting nutrient in this ecosystem. The high N concentration in roots as well as the remarkably high flux of N in litterfall (Raich *et al.*, in preparation) found in these plots indicates that N is particularly abundant. Then, it is unlikely that concentrations of this element play a main role defining turnover rates in the ecosystem. Inclusion of possible limiting elements, such as P or Ca (Vitousek, 1984), could improve our understanding of the relationship between fine-root dynamics and element concentration among tropical species.

Explaining the contrasting trends between fine-root growth and nitrogen concentration in comparison with global trends for leaves could be related to the inherent differences in metabolic functioning between those organs. Roots arise from the perycicle of a parental root, functioning as a modified stem rather than a leaf (Poorter and Berkotte, 1992; Poorter and Villar, 1997). Furthermore, metabolic activities in fine-roots such as defense, symbiotic association and interactions with rhizosphere fauna have been associated with increments in root N concentration (Langley and Hungate, 2003; Whittaker, 2003). In contrast, leaves lack of symbiotic associations and defense, at least among tropical species, seems associated with increases in leaf toughness, increasing tissue C concentration rather than N (Coley and Barone, 1996; Kursar and Coley, 2006).

In conclusion, our findings indicated that species identity might play a role in defining fine-root biomass pools in tropical ecosystems. Results suggest that root growth rates determine fine-root storage among species or that both traits are similarly controlled by an external factor. In contrast, dead root accumulation was not correlated with mortality, suggesting that necromass storage is more related with fine-root decomposition. In addition, contrasting with the global negative relationship between tissue longevity and nitrogen concentration found in leaves (Reich *et al.*, 1997), fine-root lifespan among species was not

correlated with root nitrogen concentration. Furthermore, ingrowth rates were positively correlated with root C:N ratio, which contradicts the described trend in leaves. Thus our study suggests that the assumption that fine-root demography is linked to a similar suite of traits as found in leaves may not be valid in tropical forests. We emphasize that future investigations should be focused on understanding fine-root dynamics in relation to fine-root traits rather than assuming analogies with leaves.

ACKNOWLEDGEMENTS

The authors thank Dennes Chavarría, Róger Gómez, Ricardo Bedoya, Marlon Hernández, Marvin, Eduardo and Bernal Paniagua, Joshua De Marree, and Nathan O'Leary for their assistance in the field and lab and La Selva Biological Station staff for their logistical support. Robert Stephenson provided insightful assistance in the statistical analysis and Heidi Asbjornsen and Richard Schultz provide many useful comments on an earlier draft of the manuscript. This research was funded by the U.S. National Science Foundation grant DEB-0236502.

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Table 2.1 Characteristics of the species compared in this study. Tree size corresponds to maximum tree height and mean diameter in the plantations in 2005.

Species	Family	Acronym	Tree size*	
			Height (m)	DBH (cm)
Hyeronima alchorneoides	Euphorbiaceae	HYAL	30.1	23.3
Pentaclethra macroloba	Fabaceae/Mimosoidae	PEMA	18.8	22.0
Pinus tecunumanii	Pinaceae	PITE	29.2	29.1
Virola koschnyi	Myristicaceae	VIKO	24.8	23.3
Vochysia ferruginea	Vochysiaceae	VOFE	31.0	35.4
Vochysia guatemalensis	Vochysiaceae	VOGU	33.3	31.9

*Source: http://www.nrem.iastate.edu/ECOS/species.html.

Table 2.2 Fine root biomass and necromass (g/m^2) in five soil depths and dead:live fine root-ratio for six tropical tree species in 16 yr-old single-species plantations in lowland Costa Rica. Acronyms for species are defined in Table 2.1 Values are means (standard error; n=4). Different letters indicate significant differences among species for a given depth (Tukey-Kramer HSD test; $\alpha = 0.05$).

Species Depth (cm)	HYAL	PEMA	PITE	VIKO	VOFE	VOGU
Live roots						
0-15	433 (34) ^{A}	311 (42) ^{AB}	182 (21) ^{B}	386 (42) ^{A}	247 (19) ^{B}	405 (59) ^{A}
15-30	84 (12)	86 (31)	42 (9)	71 (20)	49 (12)	78 (7)
30-50	23 (12)	16 (7)	24 (8)	47 (20)	50 (14)	40 (3)
50-75	22 (7)	43 (12)	17 (7)	44 (21)	25 (14)	38 (14)
75-100	40 (11)	30 (20)	21(4)	49 (26)	20 (11)	19 (7)
Dead roots						
0-15	125 (18) ^{AB}	93 (17) ^{BC}	48 (4) ^{D}	183 (20) ^{A}	88 (12) ^{BCD}	73 (7) ^{CD}
15-30	25 (7)	42 (17)	12 (3)	43 (14)	17 (1)	10 (2)
30-50	3 (3)	0 (0)	9 (5)	6 (3)	2 (2)	1 (< 1)
50-75	< 1 (< 1)	3 (3)	9 (4)	1 (1)	6 (5)	3 (2)
75-100	< 1 (< 1)	2 (2)	4 (3)	1 (< 1)	5 (3)	< 1 (< 1)
Dead:Live ratio						
0-100	0.26 (0.01) ^{AB}	0.28 (0.03) ^{AB}	0.29 (0.04) ^{AB}	0.40 (0.03) ^{A}	0.32 (0.06) ^{A}	0.15 (0.01) ^{B}

Table 2.3 Live fine root nitrogen and carbon mass (g/m^2) in five soil depths for six tropical tree species in 16 yr-old single-species plantations in lowland Costa Rica. Acronyms for species are defined in Table 2.1 Values are means (standard error; n=4). Different letters indicate significant differences among species for a given depth. (Tukey-Kramer HSD test; $\alpha = 0.05$).

Species Depth (cm)	HYAL	PEMA	PITE	VIKO	VOFE	VOGU
Nitrogen mass						
0-15	5.90 (0.41) ^{A}	6.43 (0.50) ^{A}	2.91 (0.29) ^{B}	6.05 (0.50) ^{A}	4.33 (0.28) ^{AB}	6.44 (0.72) ^{A}
15-30	1.15 (0.12)	1.82 (0.67)	0.68 (0.16)	1.12 (0.30)	0.85 (0.22)	1.24 (0.12)
30-50	0.28 (0.13)	0.22 (0.07)	0.27 (0.09)	0.68 (0.28)	0.48 (0.14)	0.43 (0.08)
50-75	0.24 (0.08)	0.63 (0.14)	0.11 (0.06)	0.64 (0.27)	0.24 (0.14)	0.37 (0.13)
75-100	0.41 (0.08)	0.41 (0.21)	0.25 (0.07)	0.64 (0.33)	0.21 (0.12)	0.19 (0.06)
Carbon mass						
0-15	194 (19) ^{A}	147 (14) ^{AB}	79 (7) ^{C}	181 (16) ^{A}	109 (10) ^{BC}	174 (21) ^{A}
15-30	38 (5)	41 (15)	18 (4)	33 (9)	21 (6)	33 (3)
30-50	10 (5)	7 (2)	11 (4)	22 (10)	23 (7)	17 (1)
50-75	10 (3)	19 (4)	7 (3)	21 (10)	12 (6)	16 (6)
75-100	18 (5)	13 (6)	8 (2)	23 (13)	9 (5)	8 (3)

Table 2.4 Annual fine-root ingrowth and turnover rates for six tropical species in 16-yr-old single-species plantations in lowland Costa Rica. Values are means (standard error, n=4) for the uppermost 15 cm of soil only. Different letters indicate significant differences among species (Tukey-Kramer HSD test; $\alpha = 0.05$).

Species	Ingrowth rate ($g\ m^{-2}\ yr^{-1}$)	Turnover rate (yr^{-1})	
		Biomass	Carbon
Hyeronima alchorneoides	1304 (159) ^{A}	2.98 (0.15) ^{A}	2.93 (0.19) ^{A}
Pentaclethra macroloba	641 (73) ^{BC}	2.12 (0.20) ^{AB}	2.12 (0.25) ^{AB}
Pinus tecunumanii	382 (44) ^{C}	2.21 (0.41) ^{AB}	2.21 (0.40) ^{AB}
Virola koschnyi	614 (83) ^{BC}	1.60 (0.16) ^{B}	1.56 (0.14) ^{B}
Vochysia ferruginea	518 (18) ^{C}	2.13 (0.17) ^{AB}	2.18 (0.18) ^{AB}
Vochysia guatemalensis	1068 (219) ^{AB}	2.64 (0.34) ^{AB}	2.82 (0.38) ^{A}

Table 2.5 Nitrogen and carbon concentrations and C:N for live roots in the uppermost 15 cm of six tropical species in 16-yr-old single-species plantations in lowland Costa Rica. Values are means (standard error, n=4). Different letters within columns indicate significant differences among treatments (Tukey-Kramer HSD test; $\alpha = 0.05$).

Species	N (%)	C (%)	C:N
Hyeronima alchorneoides	1.39 (0.08) ^{C}	44.7 (0.2) ^{B}	32.6 (1.5) ^{A}
Pentaclethra macroloba	2.09 (0.08) ^{A}	47.3 (0.5) ^{A}	22.8 (0.8) ^{D}
Pinus tecunumanii	1.60 (0.07) ^{BC}	43.8 (0.6) ^{B}	27.7 (1.1) ^{BC}
Virola koschnyi	1.58 (0.04) ^{BC}	46.8 (0.5) ^{A}	29.7 (0.6) ^{AB}
Vochysia ferruginea	1.77 (0.11) ^{B}	43.7 (0.7) ^{B}	25 (1.2) ^{CD}
Vochysia guatemalensis	1.59 (0.04) ^{BC}	42.8 (0.5) ^{B}	26.9 (0.6) ^{BC}

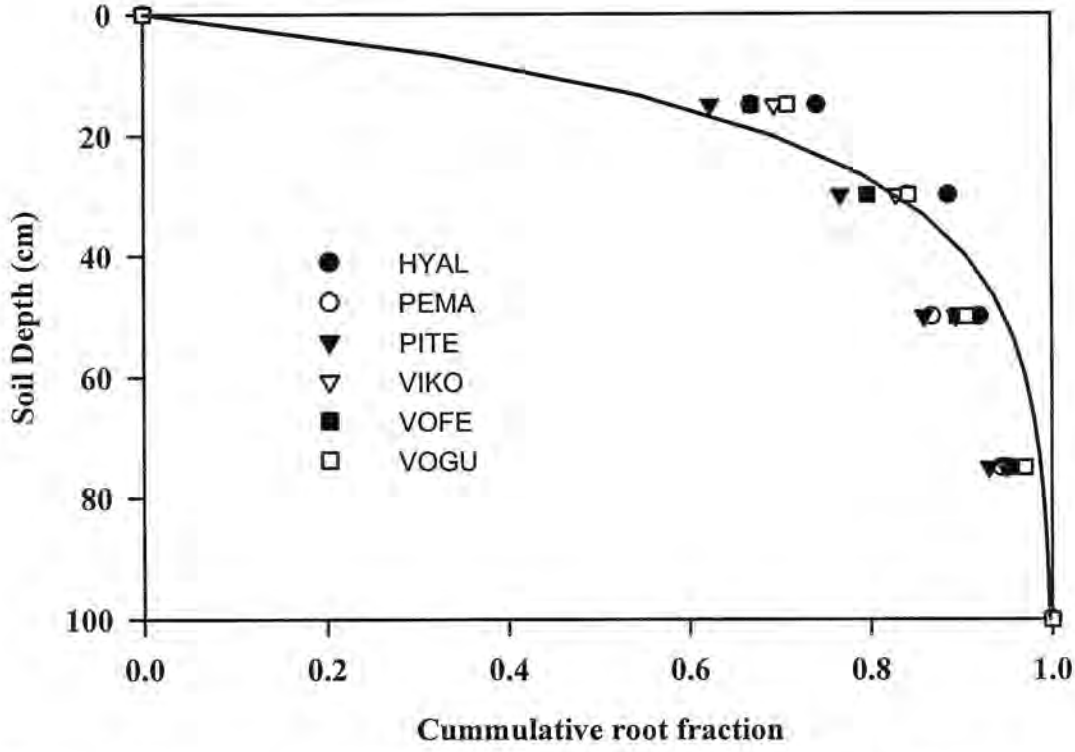

Figure 2.1 Cumulative root distribution as a function of root depth for six tropical species in 16 year-old plantations. Fit equation is $Y= 1-\beta^d$, where Y is the cumulative root fraction (proportion between 0 and 1) with depth (d in cm) and β is the fitted parameter. The curve indicates the least square fit of β for all species ($\beta = 0.943$). Acronyms for species as defined in Table 2.1.

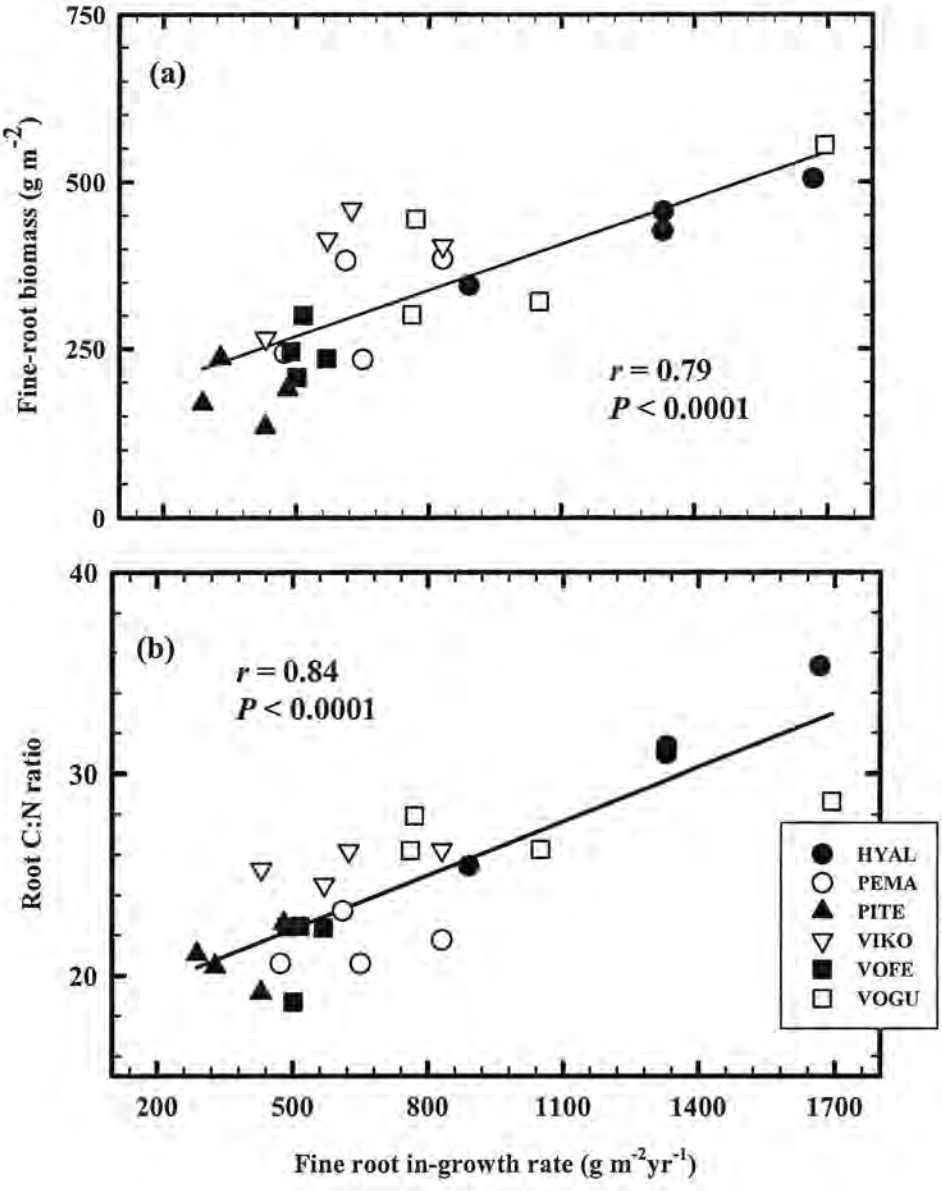

Figure 2.2 Relationship of fine-root ingrowth rates (g m^{-2} yr^{-1}) with (a) live fine-root mass (g m^{-2}) and (b) fine-root C:N ratio among six tropical tree species. Comparisons were made with mean plot values for each variable (n=24). Acronyms for species as defined in Table 2.1

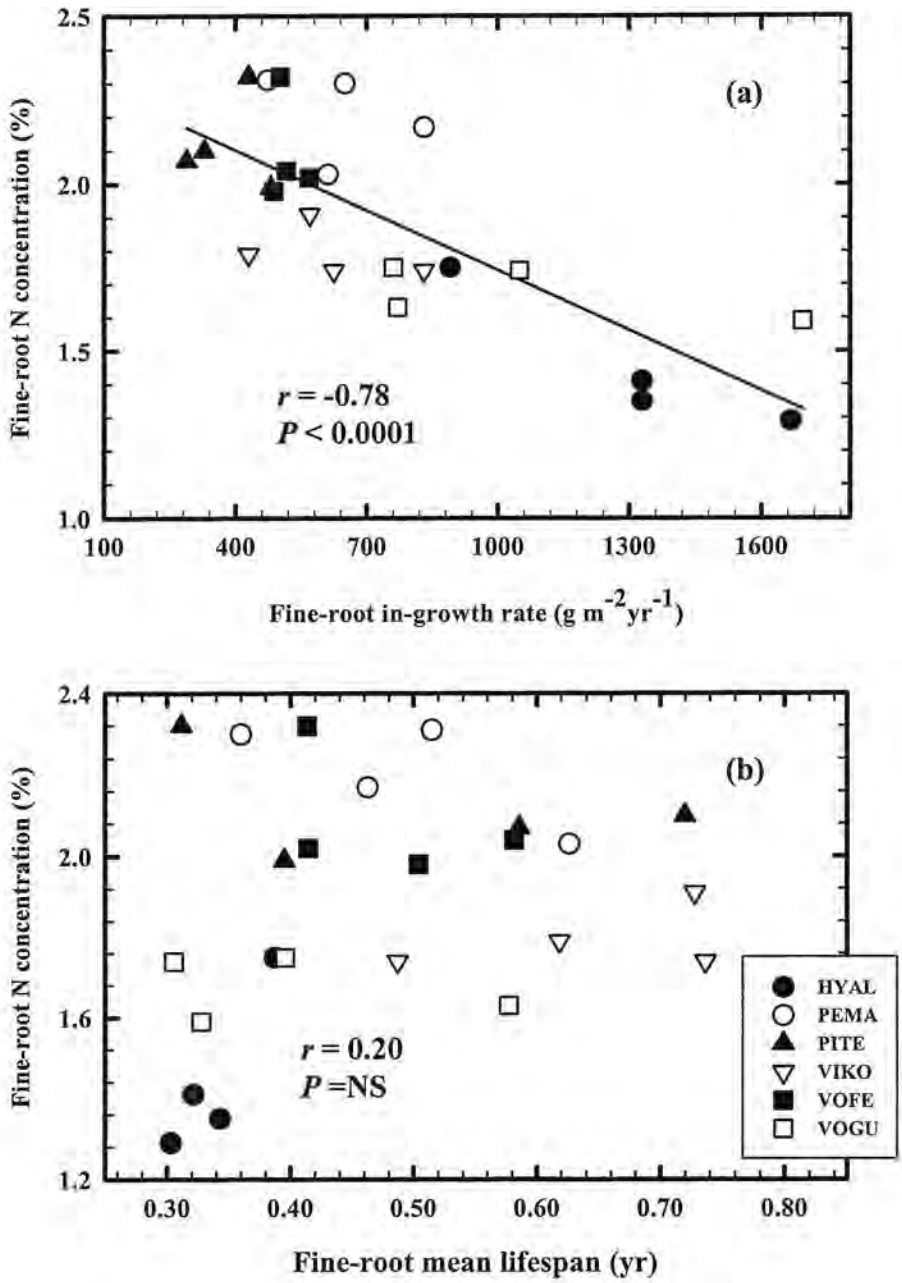

Figure 2.3 Relationship of fine-root nitrogen concentration with (a) fine-root ingrowth (g m^{-2} yr^{-1}) and (b) fine-root lifespan (yr) among six tropical tree species. Comparisons were made with mean plot values for each variable (n=24). Acronyms as defined in Table 2.1

CHAPTER 3. RELATIONSHIPS AMONG LITTERFALL, FINE-ROOT GROWTH AND SOIL RESPIRATION FOR FIVE TROPICAL TREE SPECIES

A paper to be submitted to the journal Forest Ecology and Management

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ABSTRACT

While significant advances have been made in understanding terrestrial carbon cycling at global scales, there is still large uncertainty about how carbon fluxes vary among sites at local scales, and why. In particular, little is known about how species vary in allocation to aboveground litter versus fine-root production, or how those variations affect soil-CO_2 emissions. Using a carbon mass-balance approach I investigated relationships among litterfall, fine-root growth, and soil respiration for five tree species (*Hyeronima alchorneoides*, *Pentaclethra macroloba, Pinus tecunumanii, Virola koschnyi,* and *Vochysia guatemalensis*) established as single-species, 16-year-old plantations in a randomized-block experiment ($n = 4$ blocks) in the Caribbean lowlands of Costa Rica. Total fine detritus production, i.e., litterfall plus fine root production, ranged from 690 g C m^{-2} yr^{-1} in *Virola* to 1210 g C m^{-2} yr^{-1} in *Hyeronima* with significant differences among species ($P < 0.002$) but with no correlation between litterfall and fine root growth ($P = 0.30$). Soil-CO_2 emissions ranged from 1610 g C m^{-2} yr^{-1} in *Pinus* to 2365 g C m^{-2} yr^{-1} in *Vochysia* without significant differences among species ($P = 0.08$), likely due to high spatial variability within blocks. Across plots, soil respiration increased with fine-root production at $P = 0.06$, but not with litterfall ($P = 0.26$), suggesting that soil C emissions may depend more on belowground than on aboveground detritus inputs. Estimates of root + rhizosphere respiration were high, comprising on average 52 % of total soil respiration. Comparison of belowground carbon

allocation (BCA) with fine-root growth rates indicated that on average only 27% of BCA was used to construct new tissues with the remaining 73% being respired, but fine-root carbon use efficiency increased with fine-root growth rates ($P < 0.0001$). These results suggest that inherent differences in fine-root production among species, rather than differences in aboveground litterfall, may play an important role explaining among-forest variations in soil C emissions.

INTRODUCTION

After gross primary productivity, soil respiration (R_S) is the largest flow of C in forest ecosystems (Schlesinger, 1997). Carbon dioxide is produced in soil by a variety of processes including respiration by roots and rhizosphere organisms and the decomposition of organic matter in the soil (Singh and Gupta, 1977; Raich and Schlesinger, 1992; Raich and Mora, 2005; Figure 3.1 fluxes 5 and 6 respectively). Estimates of CO_2 released by roots + rhizosphere-associated organisms (R_{rrh}) in forests range from 10 to 90 % with a mean of 46% of soil CO_2 efflux, and reflect plant activity and the supply of organic compounds from the canopy to roots (Hanson *et al.*, 2000; Figure 3.1 pathway 1-2-5). On the other hand, soil organic matter oxidation represents C that passes through the soil food web (flows 1-3+4-6 in Figure 3.1) and is related to soil organic C turnover and nutrient dynamics (Bond-Lamberty *et al.*, 2004). Although both processes occur simultaneously, their responses to environmental variables may differ (Boone *et al.*, 1998). Thus, distinguishing between those two processes (Figure 3.1, flows 5 and 6) is important to understanding variability in forest soil CO_2 emissions (Figure 3.1, flow 7).

Increasing evidence supports the view that plant production influences soil C fluxes by variation in the magnitude (Janssens *et al.*, 2001), quality (Chapin *et al.*, 1997) and allocation patterns of litterfall and fine-root C inputs into the soil (Bowden *et al.*, 1993). Despite the importance that leaf and fine-root production might have on soil respiration rates, analyses of forest ecosystems rarely include measurements of all fluxes (Matamala *et al.*, 2003), and little is known about differences among woody species in allocation patterns (Poorter and Villar, 1997). Studies conducted in tropical plantations demonstrate that species vary highly in both litterfall (Smith *et al.*, 1998; Standley and Montagnini, 1999) and fine-root growth rates (Russell *et al.*, 2004), suggesting that C allocation patterns could be strongly influenced by species identity. Cuevas *et al.* (1991), studying litterfall and root growth in parallel, found that substantial fine-root growth in a secondary forest offset high rates of aboveground productivity in a *Pinus caribaea* plantation, such that total biomass production was similar between the two stands. In the same location Li *et al.* (2005) found higher R_S rates in the secondary forest, suggesting that differences in allocation patterns might affect soil CO_2 emissions in tropical ecosystems.

Although litterfall positively relates to R_S across forest ecosystems (Raich and Nadelhoffer, 1989; Davidson *et al.*, 2002a), this trend had not been found at regional scales (Jurik *et al.*, 1991; Ruess *et al.*, 1996; Giardina and Ryan, 2002), suggesting that belowground C supply might have an important role explaining differences in soil CO_2 emission at local scales (Raich and Tufekcioglu, 2000). Nonetheless, information on belowground C allocation (BCA; flux 2, Figure 3.1) in tropical systems, as well as the partitioning of those resources to root production or respiration, is scarce (Clark *et al.*, 2001). Giardina and Ryan (2002) found that increased nutrient availability did not affect BCA

among *Eucalyptus* plantations but did decrease the fine-root mass, suggesting an increase in R_{rrh} along with a decrease in fine-root carbon use efficiency (CUE_{fr}) in root systems. Moreover, decreases in fine-root stock were related to decreases in R_S, which is consistent with trends between fine root production and soil CO_2 emissions in moist temperate forests (Campbell *et al.*, 2004). Even so, the relationship between belowground production, root respiration and soil CO_2 efflux in the tropics is still poorly understood (Nadelhoffer and Raich, 1992; Sotta *et al.*, 2004) and little is known about how species-specific differences in fine-root production could affect soil-CO_2 fluxes.

To address the mechanisms by which species may influence R_S in moist tropical forests, I studied five tropical plantations established under similar climatic and soil conditions, land-use history and management (González and Fisher, 1994). My first objective was to contrast fine-root and litter production among species. I hypothesized that litterfall rates would correlate negatively with fine-root growth and that their sum, referred to herein as total fine detritus production (TFDP; fluxes 3 + 4, Figure 3.1), would be similar among species (Cuevas *et al.*, 1991, Binkley and Ryan, 1998). Further, I hypothesized that R_S and BCA would be more related to differences in fine-root production than to differences in litterfall across plots (Campbell *et al.*, 2004). Finally, I proposed that species would have similar BCA but variable C partitioning in fine-root systems (Giardina and Ryan, 2002), such that CUE_{fr} would be positively correlated, whereas R_{rrh} would be negatively correlated, with fine-root growth across plots.

METHODS

Study site

The study was carried out from January 2004 to June 2005 in 16-year old plantations established in the biological station La Selva in the northern Caribbean lowlands of Costa Rica. The study sites were at 44-89 m elevation. La Selva has a mean temperature of 25.8 °C with minimal variation across the year. Mean annual rainfall is 3960 mm with > 150 mm of precipitation on average every month (Sanford *et al.*, 1994). The soil is classified as a Typic Tropohumult (Ultisol), which is characterized by high organic matter content, low degree of base saturation and high exchangeable acidity (Sollins *et al.*, 1994).

The site was cleared of original forest and grazed intensively for approximately 30 years until 1986. Tree plantations were established in a randomized block design in1988 (Fisher, 1995). The design contained five species in four blocks for a total of 20 plots. Each plot is 50 × 50 m. Tree spacing was originally 3 × 3 m and measurements were made inside the internal 30 × 30 m square, which was subdivided in four 15 × 15 m quadrants. For this study, the two external rows of trees in each plot were buffer areas in which no sampling was done.

The species included in this study were *Hyeronima alchorneoides* Allemao, *Pentaclethra macroloba* (Willd) Kunth., *Pinus tecunumanii* Egiluz and J. P. Perry, *Virola koschnyi* Warb, and *Vochysia guatemalensis* Donn. Sm. The five species are timber species and, excluding *Pinus*, components of the native forests in the study area (Hartshorn and Hammel, 1994). The species are planted in monocultures for timber purposes in the region (Piotto *et al.*, 2003; Petit and Montagnini, 2004) or elsewhere (Richardson, 1998). Nonetheless, the species differ in traits such as aboveground growth rates (Gonzalez and

Fisher, 1994), canopy height (Haggar *et al.*, 1997), litterfall rates (Raich *et al.*, in preparation), fine-root biomass (Valverde-Barrantes *et al.*, in preparation), and understory regeneration (Powers *et al.*, 1997). No maintenance was conducted on the plots between 1995 and 2003.

Soil Respiration

Soil surface CO_2 efflux (R_S) was measured using a portable soil respiration system (LI-COR 8100; LI-COR®, Lincoln, NE, USA) at three randomly located permanent soil collars (78.5-cm^2 area PVC collars) established in each plot, for a total of 72 collars. Measurements were conducted from October 2004 through August 2005, for a total of 792 flux measurements. A sharp knife was used to cut surface litter and soil to a depth of ~1 cm so that collars were tightly set on the soil. The condition of all collars was inspected 24 hrs before sampling, at which time all live aboveground plant tissues within collars were removed, but surface litter was left intact. Soil CO_2 fluxes for each collar and date were based on a 120-second measurement period; within chamber CO_2 concentration were recorded every second. Values were adjusted to account for actual chamber volume, based on depth of surface litter and soil collars. I estimated soil respiration rates using the LI 8100 file viewer 1.0.0 (LI-COR®, Lincoln, NE, USA). Soil respiration corresponded to the slope of the exponential fit regression adjusted to the CO_2 concentration increase in the chamber during 100 seconds, considering the initial 20 seconds as a dead-band margin.

Litterfall and ingrowth rates

Aboveground litter production measurements for the calendar year 2004 were

described by Raich *et al.* (in preparation). Briefly, aboveground litter was trapped in four 1.3 × 0.4 m baskets per plot for one year. Every two weeks the material from each plot, including branches ≤1 cm in diameter, was oven dried at 65 °C and weighed. Fine-root biomass and growth rates were reported by Valverde-Barrantes *et al.* (in preparation). Fine-root growth rates were determined using the ingrowth-core technique (Russell *et al.*, 2004). Five 15-cm deep, 5.4-cm diameter ingrowth cores were installed in each plot. Cores were installed and removed every four months systematically from June 2004 through June-July 2005. Neither overstory litter nor fine root samples were identified to species, so it must be noted that the treatment effect 'species' refers to the whole plot and all the ways that the overstory dominants may influence site physical, chemical and biological processes, and including the contribution from understory regeneration. However, most plots were closed-canopy plantations with monospecific overstories; overstory leaves comprised more than two-thirds of the total leaf production in all species (Raich *et al.*, in preparation). Carbon concentration in litter tissues was determined using a CE Elantech Flash EA 1112 C-N elemental analyzer.

Belowground carbon allocation and root rhizosphere respiration.

There are many difficulties associated with direct measurements of BCA or rhizosphere activities, which include root sloughing, exudation and symbiotic maintenance (Eissenstat and Yanai 1997; Farrar and Jones, 2003). The carbon mass-balance approach (Raich and Nadelhoffer, 1989; Raich, 1998; Davidson *et al.*, 2002a; Giardina and Ryan, 2002) was employed in this study. Considering the uppermost litter layer as part of the soil carbon pool, carbon outputs from the soil equal carbon inputs plus any change in storage over a period of

time (Raich and Nadelhoffer, 1989; Giardina and Ryan, 2002). In nearly steady state soil systems C inputs such as litterfall and BCA, would be similar to soil-C emissions (R_S), the main output (See Figure 3.1). Thus, BCA can be estimated as soil-C emissions minus the aboveground litterfall C flux (Raich and Nadelhoffer, 1989; Figure 3.1):

$$BCA \approx R_S - LF \quad (1)$$

where BCA = total C allocated to fine-root growth and root + rhizosphere respiration (fluxes 4 and 5, Figure 3.1); LF = aboveground litterfall (flux 3, Figure 3.1); and R_S = soil-C emissions. Parallel studies at the same study site demonstrated that total fine-root biomass (Valverde-Barrantes *et al.*, in preparation) and surface litter (Raich *et al.*, in preparation) did not vary significantly between two years of measurement and that soil organic matter accumulation rates were small to nil (Russell *et al.*, submitted). Changes in coarse root biomass were not considered in this study, which focuses on C turnover (vs. accumulation) in the soil, but coarse root growth can contribute substantially to total BCA (TBCA, Giardina and Ryan, 2002). Note, however, that estimates of R_{rrh} (below) include respiration from woody roots.

Root + rhizosphere respiration was estimated using the equation

$$R_S = R_{som} + R_{rrh} \quad (2)$$

where R_S = the average annual CO_2 efflux rate, R_{som} = the product of respiration by soil decomposers and R_{rrh} = root + rhizosphere respiration (i.e. fine and coarse root respiration,

root exudation and mycorrhizae maintenance). Given no significant changes in soil C (Russell *et al.*, submitted), surface litter (Raich *et al.*, in preparation) or fine-root stocks on an annual basis (Valverde-Barrantes *et al.*, in preparation), C inputs from detritus production must be similar to C outputs produced by soil organic matter oxidation (Raich and Nadelhoffer, 1989; Davidson *et al.*, 2002a). So, R_{som} is approximately equal to the sum of annual fine-root growth and aboveground litter production (TFDP; fluxes 3 + 4 ≈ flux 6, Figure 3.1), whereas R_{rrh} is approximately the difference between R_S and R_{som} (flux 5 ≈ flux 7 - flux 6, Figure 3.1).

Carbon use efficiency in the fine-root system was estimated as the fraction of BCA allocated to fine-root growth:

$$CUE_{fr} = FRG/BCA \quad (3)$$

where CUE_{fr} = carbon use efficiency in fine roots, FRG = fine root growth rate (flux 4, Figure 3.1), and BCA = belowground carbon allocation (flux 2, Figure 3.1). Species total detritus production, belowground carbon allocation and root + rhizosphere respiration were estimated using the average of each variable in each plot.

Data analysis

Plot-level R_S for each sampling date was calculated as the mean value of all measurements within the plot. Measurements through time were analyzed with a repeated-measure ANOVA with species, block and date and their interaction as main factors and plot-level R_S as response. To address my first hypothesis, species differences in total fine detritus

production, i.e., fine-root growth plus aboveground fine litterfall, were determined using ANOVA with species and block as the main factors, followed by pair-wise comparisons using Tukey-Kramer HSD tests ($\alpha = 0.05$). I determined the relationship between fine-root ingrowth and litterfall with correlation analysis using mean values of each variable at the plot level ($n = 20$). To address hypothesis two, I performed linear regression analyses among fine-root growth, litterfall and total detritus production with R_S at the plot level ($n = 20$). For the third hypothesis, I performed ANOVA with species and block as the main factors and the fine-root BCA as response variable. Finally, correlation analyses were performed to determine the relationship between fine-root growth with R_{rrh} and with CUE_{fr}. All statistical analyses were performed using JMP Data Analysis software (version 5.1.2, SAS Institute, NC, USA)

RESULTS

Carbon partition between above- and belowground compartments

Species differed in terms of total fine detritus production (TFDP) (ANOVA; $P < 0.002$; Table 3.1). *Hyeronima* plots, with 1210 g C m^{-2} yr^{-1}, had the highest TFDP, but not significantly higher than that in *Vochysia* plots, whereas *Pinus* and *Virola* plots had a TFDP significantly lower than that showed for the two most productive species (Tukey-Kramer HSD, $P < 0.05$; Table 3.1). Indeed, *Hyeronima* plots produced on average 1.8 times more detritus that *Virola* plots, refuting the hypothesis that species would show similar TFDP. The ratio between aboveground and belowground fine litter production also varied among species (ANOVA; $P < 0.001$; Table 3.1). Aboveground litterfall and fine-root growth rates were

similar in *Hyeronima, Vochysia* and *Virola* plots, resulting in a fine-root growth:litterfall ratio relatively close to 1. In contrast, *Pentacletha* and *Pinus* allocated relatively more resources to aboveground litter production (Tukey-Kramer HSD, $P < 0.05$; Tabel 3.1). Across plots, aboveground litterfall was not correlated with fine-root ingrowth ($r = 0.19$; n = 20; $P = 0.30$). These results did not support the hypothesis that belowground detritus production offset aboveground litterfall differences among species.

Soil respiration and detritus inputs

Soil-CO_2 emissions ranged from 1610 g C m^{-2} yr^{-1} in *Pinus* plots to 2365 g C m^{-2} yr^{-1} in *Vochysia*, with 1980 g C m^{-2} yr^{-1} as the overall average among species (Figure 3.1). Estimates of R_S were higher than that for moist tropical forests (1260 ± 57 g C m^{-2} yr^{-1}) reported by Raich and Schlesinger (1992) or the average (1480 g C m^{-2} yr^{-1}) mentioned by Schwendenmann (2002) on residual soils of La Selva. Nonetheless, they were similar to those reported in *Eucalyptus* plantations (Giardina and Ryan, 2002; Binkley *et al.*, 2006) and Amazonian forests established on highly degraded soils (Davidson *et al.*, 2000). I did not detect a significant difference in R_S among species ($P = 0.08$) or blocks ($P = 0.60$) but found a significant interaction among plots (ANOVA; species × block, $P < 0.0001$), indicating that R_S within species was substantially influenced by plot conditions. Furthermore, the sample size was probably insufficient to detect significant differences among species. Soil respiration in tropical forest soils is particularly variable (Trumbore *et al.*, 2006) and detecting differences with an error in the mean of no more than 10% in soil–surface CO_2 efflux requires sample sizes ranging from 40 to 85 measurement points (Davidson *et al.*, 2002b; Adachi *et al.*, 2005), which is substantially higher than the 12 measurements per

species considered in this study.

Pentaclethra plots had the largest variation ranging from 1332 and 2422 g C m^{-2} yr^{-1} (coefficient of variation CV = 26%). The remaining species showed variations between 10 and 20%, which is similar to previous coefficients of variation reported for R_S in La Selva unaltered forests (Schwendenmann, 2002). *Vochysia* plots showed relatively high values, ranging from 2140 to 2600 g C m^{-2} yr^{-1} whereas *Virola* had lower values ranging from 1685 to 2040 g C m^{-2} yr^{-1}. Soil-CO_2 emissions rates also varied significantly through time ($P < 0.0001$). Rates were lowest in November 2004, then fluctuated until June 2005 when they started to increase, reaching the highest values in August 2005. This pattern is similar to previous temporal variation recorded in La Selva unaltered forests and it seems to be related to patterns in precipitation (Schwendenmann, 2002; Sanford *et al.*, 1994)

Soil-CO_2 emissions were related with total fine detritus production ($r^2 = 0.20$; n = 20; $P = 0.05$) and marginally related with fine-root ingrowth rates ($r^2 = 0.17$; n = 20; $P = 0.06$), but not to litterfall ($r^2 = 0.06$; n = 20; $P = 0.26$; Figure 3.2). Carbon allocation to fine roots was not related to litterfall ($r^2 < 0.01$; n = 20; $P = 0.92$) or fine-root ingrowth ($r^2 = 0.13$; n = 20; $P = 0.12$). One of the *Hyeronima* plots stands out as having low R_S for the fine-root ingrowth rates. This could be related to the presence of a large leaf-cutter ant nest (*Atta cephalotes*) close to two of the three collars set in the plot. Comparison of R_S between ant nests and unaltered soils showed that ant nests had on average 20% lower CO_2 emission rates than unaltered areas under the same species (*Vochysia* plots, t-test; $P < 0.001$; data not shown). Although the *Hyeronima* plot was not identified as an outlier by the studentized residual, when this point is omitted from the regression between fine-root ingrowth and R_S the r^2 value increases from 0.17 to 0.34, the P value decrease from 0.06 to 0.009 and the

slope of the regression changed from 0.9 to 1.4. Similarly, the r^2 value in the regression between BCA and fine-root ingrowth increases from 0.13 to 0.27, the *P* value decrease from 0.12 to 0.02 and the slope of the regression changed from 0.17 to 0.23. In summary, the results supports the prediction that R_S and BCA are more related to fine-root production than to aboveground fine litterfall across plots.

Among species, aboveground fine litterfall inputs comprised on average 30 % of the annual R_S, which is consistent with the proportion estimated for mature forests across biomes (Davidson *et al.*, 2002a). Fine-root detritus contributed on average 19% of the annual R_S among species but varied from only 11% in *Pinus* to 30 % in *Hyeronima* plots. Annual detritus production supplied approximately 48% of the annual soil C emissions. *Virola* was the species where detritus production had the lowest contribution to soil C emissions, comprising on average 38% of the annual R_S. In contrast, *Hyeronima* detritus production accounted for 62% of the annual R_S in those plots, being significantly higher that the proportion in *Virola* plots (ANOVA, $P = 0.04$; data not shown), which further implies that the proportion of R_S provided by R_{rrh} was also different between these two species. The proportion of R_{rrh} to annual R_S was on average 52%, which is similar to estimations of root respiration contribution to soil CO_2 efflux in temperate forests (Högberg *et al.*, 2001; Fahey *et al.*, 2005)

Belowground carbon fluxes

Supporting the proposed hypothesis, estimates of BCA were not significantly different among species (ANOVA; $P = 0.07$; Figure 3.1), although the flux in *Vochysia* plots was on average 58% higher than values found in *Pinus* plots. Average R_{rrh} was 1010 g C m^{-2} yr^{-1}

among plots, ranging from 825 g C m^{-2} yr^{-1} in *Hyeronima* plots to 1335g C m^{-2} yr^{-1} in *Vochysia* plots, without significant differences among species (ANOVA; $P = 0.24$; Figure 3.1). On the other hand, CUE_{fr} varied significantly among species (ANOVA; $P = 0.01$; Table 3.1). *Hyeronima* plots had the highest CUE_{fr} and were significantly higher than the values observed in *Pinus* plots (Tukey-Kramer HSD, $P < 0.05$; Figure 3.1). Among species average CUE_{fr} was 0.28 ± 0.09, which is lower than the 0.39 ± 0.03 mentioned by Litton *et al.* (2006) but similar to estimations of CUE in tropical ecosystems (Chambers *et al.*, 2004). Across plots, fine root ingrowth was positively correlated with CUE_{fr} ($r = 0.82$; n = 20; $P < 0.0001$; Figure 3.3) but uncorrelated with R_{rrh} ($r = 0.13$; n = 20; $P = 0.59$; Figure 3.3). These results support the hypothesis that CUE_{fr} would be positively correlated with fine-root growth but not the proposed negative correlation between fine-root growth and R_{rrh}.

DISCUSSION

Annual detritus production and allocation patterns

Among species, differences were larger in root production than in litterfall. For instance *Hyeronima* plots, which had the highest litterfall rates, produced on average 1.6 times more litter than *Virola* plots (Raich *et al.*, in preparation) whereas *Hyeronima* plots produced 3.4 times more fine-roots than *Pinus* plots, the species with the lowest fine-root growth rates (Valverde-Barrantes *et al.*, in preparation). There was no trade-off between above and belowground productivity among species contrary to the hypothesis that species would show an offset between litterfall and fine-root growth (Cuevas *et al.*, 1991; Binkley and Ryan, 1998). *Pinus* plots had a contrasting pattern in comparison with the broadleaf

species, exhibiting a litterfall production three times higher than fine-root growth rates. The low belowground-high aboveground productivity reported for *Pinus* plantations in this study correspond with previous reports in tropical plantations (Cuevas *et al.*, 1991; Cavalier and Santos, 1999) and is possibly related to intrinsic differences in resource acquisition, symbiotic associations, and nutrient use efficiency between this genus and most tropical trees (Hobbie, 2006). The remaining species were relatively similar in terms of the fine-root:litterfall ratio (Table 3.1), suggesting that broadleaf species in tropical ecosystems vary in their total detritus productivity but not in allocation patterns. Differences in biomass production among the studied species have been mentioned previously (González and Fisher, 1994; Haggar and Ewel, 1997; Iriarte and Chazdon, 2003; Russell *et al.*, 2004), suggesting an inherent capacity of some species, such as *Hyeronima* and *Vochysia*, to produce more fine detritus than others. Nonetheless, confounding factors such as understory contribution to total production, limit the scope of this conclusion.

Soil respiration and annual detritus inputs

Several studies had found a positive relationship between detritus production and R_S at global scales (Raich and Nadelhoffer, 1989; Bond-Lamberty *et al.*, 2004). However, most of the information about detritus production is limited to litterfall rates, which seem to be unrelated to R_S at smaller scales (Davidson *et al.*, 2002a). Belowground measurements have been scarcely considered in most forest C-flux studies, although belowground processes might contribute with 50-90% of the annual soil CO_2 efflux (Hanson *et al.*, 2000). In addition, studies in tropical forests indicated that sites with evident differences in soil

moisture regimes or fertility showed substantial differences in fine-root growth but similar litterfall rates (Cuevas and Medina, 1988; Sanford and Cuevas, 1996), suggesting that fine-root dynamics is a better indicator of site variation at regional scales. Therefore, I considered that variation in R_S and BCA would be related to differences in fine-root production rather than variation in fine litterfall among sites dominated by different species.

Campbell *et al.* (2004) found that belowground productivity influenced R_S rates across coniferous forests established in a wide range of precipitation, temperature and succesional stages, suggesting that both fluxes are similarly influenced by abiotic constraints. Sanford and Cuevas (1996) mentioned that a moist tropical forest on a highly weathered soil had higher fine-root mass and production than a younger alluvial soil but similar litterfall rates. Moreover, the site with higher root production had also higher R_S rates, suggesting a link between belowground production and soil CO_2 emissions (Schwendenmann, 2002). Dornbush (2005) detected also that R_S among various temperate grassland species was governed more by belowground carbon allocation than aboveground production, remarking the influence that species identity may exert on belowground biotic processes. In agreement with this evidence, R_S in this study was significantly and positively related to fine-root ingrowth rates across all plots whereas there was no relationship between aboveground fine litter production and R_S, pointing out fine-root dynamics as an important factor to understand the variation in R_S at local scales.

The large annual R_S in this study, in comparison with the range of published values for tropical moist forests (Raich and Schlesinger, 1992) likely relates to the high productivity of forest plantations in the moist tropics (Evans and Turnball, 2004) and suggest that these species may allocate large quantities of C belowground. Similarities among species in BCA

support the hypothesis that species allocate equally high amounts of C belowground. However, this conclusion must be considered with precaution due the marginality of the differences (P = 0.07). Particularly *Pinus* plots showed low BCA values, suggesting that this species allocate lower amounts of C belowground in comparison with the other broadleaf species. This pattern is consistent with the differences in root production and probably related to contrasting patterns in belowground resource acquisition between coniferous and broadleaf species, as mentioned before. The similarities in BCA among the native species are consistent with studies that compared plantations (Giardina and Ryan, 2002) or primary and secondary forests located in tropical lowlands (Salimon *et al.*, 2004), suggesting that tropical forest ecosystems in general, allocate a substantial amount of resources belowground, and that the total amount of C allocated belowground is similar among sites despite the differences observed in fine-root production.

Root + rhizosphere respiration and carbon use efficiency

Fine-root growth averaged 27% of BCA, although this value could be underestimated regarding the possible sink of C in coarse roots. Even so, this low CUE_{fr} is expected in shallow fine-root systems exposed to high temperatures, low fertility and physical damage that increase maintenance costs (Atkin *et al.*, 2000; Eissenstant *et al.*, 2000; Chambers *et al.*, 2004). Considering the similarities among species in BCA, I hypothesized a trade-off between CUE_{fr} and R_{rrh}, which was partially supported by my results. Carbon use efficiency in fine roots increased with fine-root ingrowth rates, but this was not associated with a decrease in R_{rrh}. The reason for this inconsistency could lie in the compensation observed between root mass and root respiration (Lambers *et al.*, 1996). Species with low fine-root

growth rates maintain higher root respiration rates per unit of mass than do fast-growing species (Poorter *et al.*, 1990), which is consistent with this study. However, this difference in respiration per unit of mass is compensated by the higher amount of biomass in fast-growing species, resulting in a similar amount of C released at the ecosystem level. This pattern was also found in fine-root N content in a parallel study (root N concentration varied among species but differences were compensated by variations in root biomass; Valverde-Barrantes et al., in preparation). Eissenstat *et al.* (2000) and Ryan *et al.* (2004) indicated that N content strongly correlates with tissue maintenance respiration. Thus, if the amount of N is a good indicator of metabolic activity in the root system, similarities in belowground N content among species would explain the similarities in R_{rrh} at the ecosystem level. Even so, lack of correlation between root respiration and fine-root growth rates had been reported in temperate species as well (Comas and Eissenstat, 2004), evidencing the complicated relationship between growth rates and metabolic activities in fine roots.

Efflux of CO_2 from the soil is the main output term of the soil C budget. However, the inability to distinguish among the predominant processes producing CO_2 within soils limits the interpretation of R_S data. The model used in this study provided values for heterotrophic decomposition (48%) and root-rhizosphere respiration (52%) that are comparable with previous attempts based on alternative methodologies such as root-litter exclusion (Bowden *et al.*, 1992; Li *et al.*, 2004), isotope composition of CO_2-C (Trumbore *et al.*, 2006) or tree-girdling (Högberg *et al.*, 2001; Binkley *et al.*, 2006). Thus this budgetary mass-balance estimate can be useful to determine the partitioning of soil CO_2 flux into its main sources, improving our capacity to understand soil C-soil dynamics. Findings indicated that tropical tree species vary in fine-root growth rates and therefore, the amount of detritus

entering the soil. Regarding that root production and rhizosphere activities may exert contrasting effects on microbial and soil carbon dynamics (Dornbush, 2005; Chen *et al.*, 2006) it is likely that dominant species influence in many ways soil C pools in tropical regions (Russell *et al.*, 2004; Li *et al.*, 2005) and the subsequent release of C from the soil. Further research must focus on the possible environmental factors that affect species root + rhizosphere respiration and microbial degradation of soil organic detritus at local scales.

In summary, two main conclusions emerge from this study. First, fine root production is not related to aboveground fine litter production among tropical tree species. Along with Litton *et al.* (2006) who evidenced poor correlations between aboveground biomass and TBCA among forest ecosystems, this study indicates that fine-root dynamics is not a complementary compartment or a passive mirror of aboveground litter production among tropical tree species. Therefore, future understanding of fine-root dynamics in tropical areas will require direct belowground measurements rather than indirect estimations based on aboveground observations. Second, species differences belowground influence soil-C processes. Results in this study indicate that soil-C emissions are positively linked with fluxes of fine-root productivity but not with aboveground litter production, highlighting the importance of fine-root dynamics on belowground processes. This study reinforce the idea that species differences in fine-root productivity, tissue chemistry and turnover may influence not only soil-C stocks (Russell *et al.*, 2004) but also soil CO_2 emissions in tropical ecosystems.

ACKNOWLEDGEMENTS

The author thank Dennes Chavarría, Róger Gómez, Ricardo Bedoya, Marlon Hernández, Marvin, Eduardo and Bernal Paniagua, Joshua De Marree, and Nathan O'Leary for their assistance in the field and lab and La Selva Biological Station staff for their logistical support. James Raich, Ann Russell and Robert Stephenson provided insightful assistance in the statistical analysis and revision of the manuscript. This research was funded by the U.S. National Science Foundation grant DEB-0236502

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Table 3.1 Total fine detritus production (TFDP; i.e. aboveground litter plus fine-root growth), fine-root ingrowth:aboveground litterfall ratio (FRG:LF), soil respiration (R_S), rhizosphere respiration (R_{rh}), belowground carbon allocation (BCA), and fine-root carbon use efficiency (CUE_{fr}) for five tropical species in 16-yr-old single-species plantations located in the Caribbean lowlands of Costa Rica. Values are means (standard error, n = 4). Different letters indicate significant differences among species (Tukey-Kramer HSD test; $\alpha = 0.05$). Acronyms for species: *Hyeronima alchorneoides* HYAL, *Pentaclethra macroloba* PEMA, *Pinus tecunumanii* PITE, *Virola koschnyi* VIKO, *Vochysia guatemalensis* VOGU.

Species	HYAL	PEMA	PITE	VIKO	VOGU
TFDP ($g\ C\ m^{-2}\ yr^{-1}$)	1210 (59) ^{A}	880 (50) ^{BC}	720 (31) ^{C}	690 (53) ^{C}	1030 (120) ^{AB}
FRG:LF	0.93 (0.17) ^{A}	0.53 (0.06) ^{AB}	0.32 (0.07) ^{B}	0.70 (0.10) ^{AB}	0.88 (0.15) ^{A}
R_S ($g\ C\ m^{-2}\ yr^{-1}$)	2030 (220)	1770 (230)	1610 (145)	1800 (85)	2365 (70)
R_{rh} ($g\ C\ m^{-2}\ yr^{-1}$)	825 (260)	895 (235)	890 (110)	1110 (45)	1335 (120)
CUE_{fr}	0.45 (0.10) ^{A}	0.28 (0.05) ^{AB}	0.16 (0.03) ^{B}	0.20 (0.02) ^{AB}	0.27 (0.05) ^{AB}
BCA ($g\ C\ m^{-2}\ yr^{-1}$)	1400 (235)	1200 (210)	1060 (110)	1395 (70)	1830 (110)

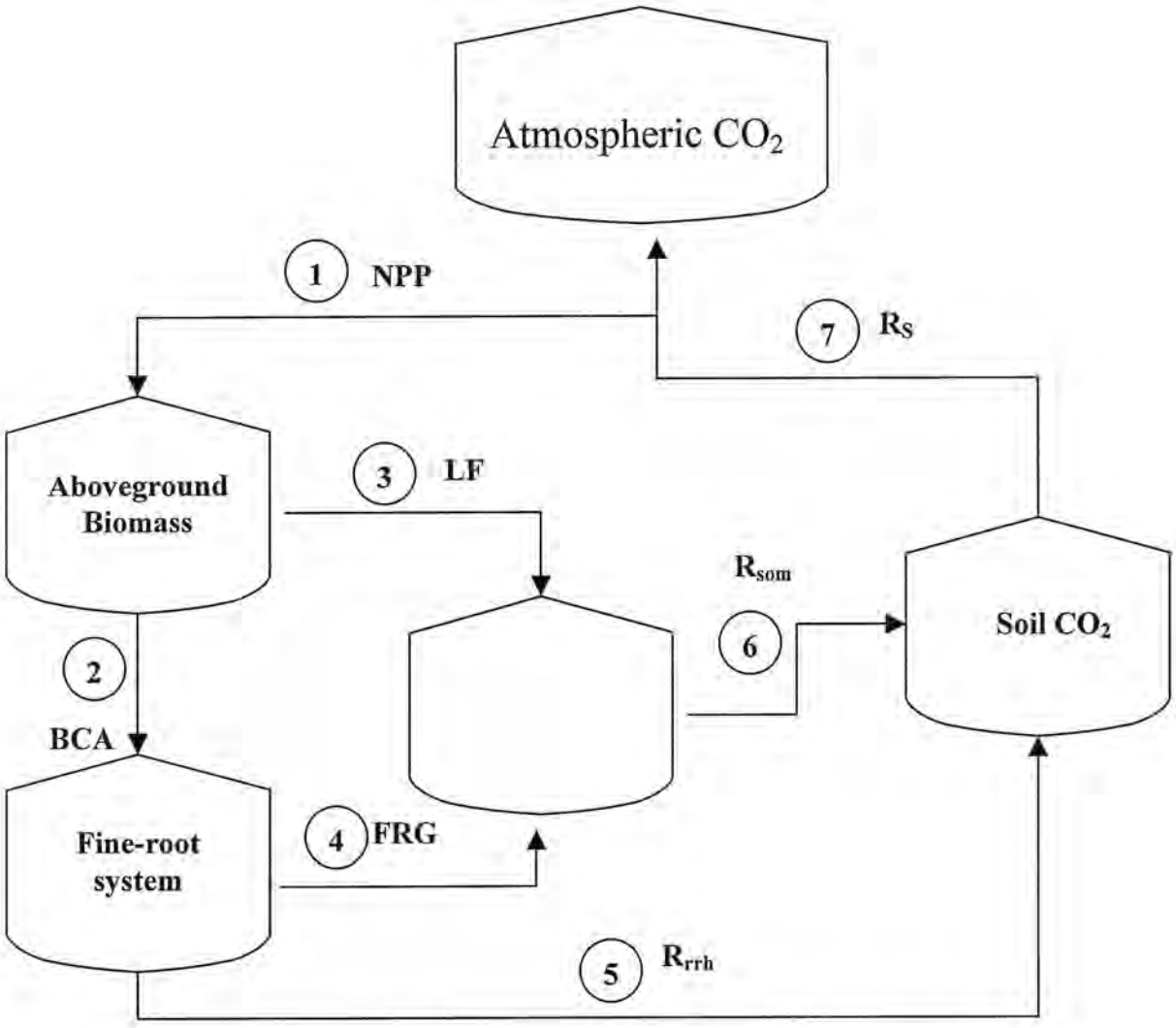

Figure 3.1. Carbon pools and fluxes through the studied plantations. 1) NPP = Net primary productivity. 2) BCA = Carbon allocated to root systems, estimated in this study as the soil respiration minus aboveground litterfall (Eq.1). 3) LF = Aboveground litterfall. 4) FRG= Fine root growth rate, which is similar to fine-root detritus inputs because fine-root systems are in steady state (see text). 5) R_{rrh}= Root, mychorrizal and rhizosphere respiration, estimated in this study as the soil respiration minus soil organic matter decomposition (Eq. 2). 6) R_{som}= CO_2 produced by soil organic matter decomposition, which equals total fine detritus production in this study (see text). 7) R_S= Soil respiration.

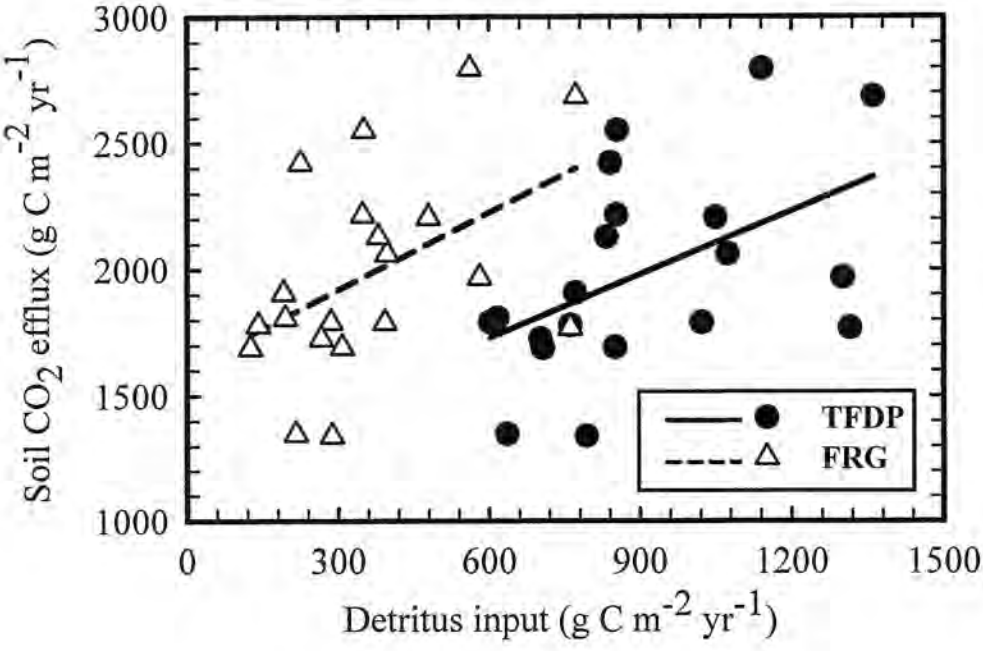

Figure 3.2 The relationships between fine-root detritus production (FRG) and total fine detritus production (i.e. aboveground litterfall plus fine-root detritus production; TFDP) with annual soil CO_2 efflux for five tropical tree species established as plantations in the Caribbean lowlands of Costa Rica. Each point represents average values for each plot (n= 20). Soil-CO_2 emissions were related with total fine detritus production ($r^2 = 0.20$; $P = 0.05$) and marginally related with fine-root ingrowth rates ($r^2 = 0.17$; $P = 0.06$), but not with litterfall ($r^2 = 0.06$; $P = 0.26$; data not shown).

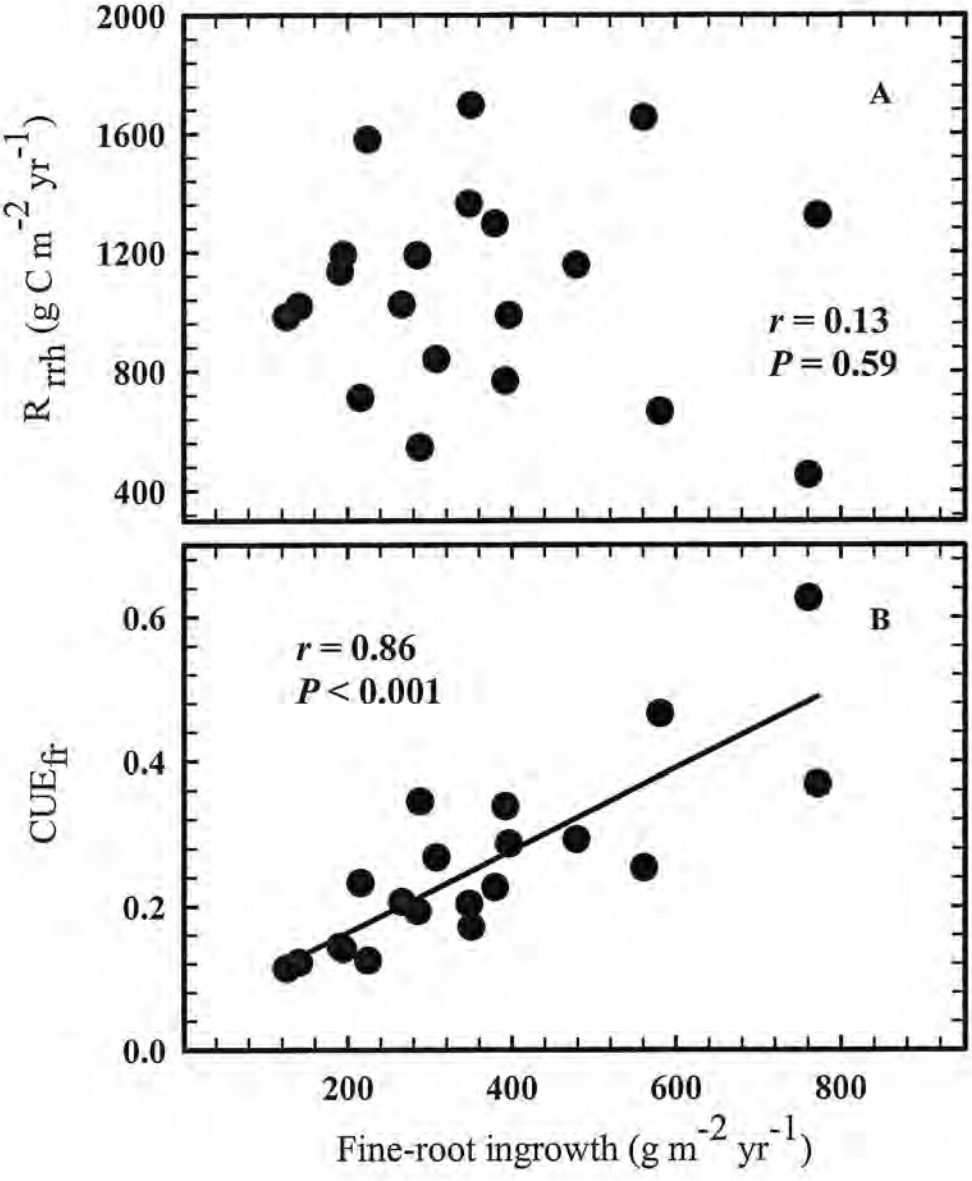

Figure 3.3 The relationship between A) root + rhizosphere respiration (R_{rrh}) and B) fine-root carbon use efficiency (CUE_{fr}) with fine-root ingrowth rates for five tropical tree species established as plantations in the Caribbean lowlands of Costa Rica. Each point represents average values for each plot (n= 20).

CHAPTER 4. GENERAL CONCLUSIONS

Throughout this thesis I provided evidence that fine root systems differ among tropical tree species. In chapter two I determined that fine root systems differed in mass, growth rates, longevity and nitrogen and carbon concentration. Live fine-root mass was correlated with ingrowth rates, suggesting that root growth rates determine fine-root storage among species or that both traits are similarly controlled by an external factor. In contrast, dead root accumulation was not correlated with mortality, suggesting that necromass storage is more related with fine-root decomposition. These findings indicated that species identity may play a role in defining fine-root biomass pools in tropical ecosystems. However, those differences were evident only in the upper 15 cm of the soil. An increase in clay under this layer seems to impede fine root growth deeper in the profile. Thus, soil physical conditions appeared as an important factor in determining fine root vertical distribution in these soils, overriding specific differences in fine root production. I also tested the published suggestion that fine roots and leaves are analogous in terms of the relationship among tissue nitrogen-carbon status, growth rates and longevity (Eissenstat and Yanai, 1997; Reich *et al.,* 1998). My results did not support this position. In fact, the relationship between fine-root growth and C:N ratio was opposite to the trend expected for foliar tissues. These results suggest further investigations searching for potential factors controlling fine-root longevity and growth rates in tropical species should be done.

In chapter three I described the relationships among fine root growth, aboveground litter production and soil respiration, all fluxes in the ecosystem carbon cycling. I tested the hypothesis that fine root growth would offset differences in aboveground litter production among species (Cuevas *et al.*, 1991; Binkley and Ryan 1998). In addition, using mass

balance principles (Giardina and Ryan, 2002), I wanted to determine if detritus carbon inputs to the soil would be positively related to soil respiration (Raich and Nadelhoffer, 1989), and whether rhizosphere respiration would be negatively correlated with fine-root ingrowth (Lambers *et al.*, 1996). My results did not find an offsetting effect among species in detritus production. Instead, species such as *Hyeronima alchorneoides*, produced high amounts of both aboveground litter and fine roots, whereas *Virola koschnyi* had low production in both fluxes. I conclude that tropical tree species vary substantially in detritus production rates. Soil respiration was weakly related with fine-root detritus inputs to the soil. Nonetheless, soil-C emissions were both spatially and temporally variable, suggesting that site conditions affect substantially the variability in soil respiration rates. Rhizosphere respiration was similar among species and not related to fine-root growth rates. Similarities in rhizosphere respiration offset differences in fine-root ingrowth among species and the belowground carbon allocation flux did not vary significantly among species. These results suggested that metabolic activity is similar among fine-root systems despite the differences observed on fine-root production.

The range of traits showed by fine-root systems in this study point out the complexity of tropical root systems. Differences in root growth among species, as well as the potential differences in fine-root decay, suggest that species identity may exert an important role on belowground processes such as nutrient availability or soil organic carbon accrual. Further research should investigate the physiological differences in fine roots and the effect of those differences in ecosystem biogeochemistry. This study also revealed rhizosphere respiration as an important flux in tropical fine root systems. Thus, future research in tropical fine-root

systems should explore the role of root respiration and symbiotic associations in tropical species and its implication in belowground carbon allocation patterns.

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